UNIVERSITÉ DU QUÉBEC À MONTRÉAL

DIVERSITY MEETS DECOMPOSITION IN FRESHWATER STREAMS: TESTING FOR A 'HOME FIELD ADVANTAGE' IN FRESHWATER DECOMPOSER COMMUNITIES IN A BOREAL VERSUS A TEMPERATE HARDWOOD STREAM

THESIS

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UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LA RELATION ENTRE LA BIODIVERSITÉ ET LA DÉCOMPOSITION DANS LES RUISSEAUX D'EAU DOUCE: TESTER L'HYPOTHÈSE DE 'HOME FIELD ADVANTAGE' DANS LES COMMUNAUTÉS DE DÉCOMPOSEURS DANS UN RUISSEAU BORÉAL PAR RAPPORT UN RUISSEAU DE LA FORÊT FEUILLUE

MÉMOIRE

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BP	Bacterial Production (μC $L^{-1}day^{-1}$)
Chl*a*	Chlorophyll *a* (μg/L)
Conductivity	Conductivity (μS/cm)
DOC	Dissolved Organic Carbon (mg/L)
TN	Total Nitrogen (mg/L)
TP	Total Phosphorus (μg/L)

RÉSUMÉ

La décomposition en ruisseaux d'eau douce est un processus écosystémique reliant la végétation riveraine, l'environnement physico-chimique, et les communautés d'organismes décomposeurs. Cependant, le lien entre la décomposition et la diversité de la communauté des organismes décomposeurs n'est pas bien comprise. L'objectif de notre étude était de tester les relations entre la diversité de la communauté des décomposeurs et la décomposition sous des conditions locales en utilisant les sources regionals de feuilles mortes dans les cours d'eau. Nous avons testé si les macroinvertébrés sont localement optimisés pour décomposer la litière de feuilles locale en comparaison à la litière de feuilles de source regionale («home field advantage») dans deux petits ruisseaux similaires. Durant l'été 2014, nous avons mené une expérience de transplantation de terrain réciproque de patron factoriel 2 x 2 avec des sacs de feuilles mortes composés d'aulne rugueux (*Alnus incana rugosa*) de chacune des sources régionales suivantes: un ruisseau boréal vierge et un ruisseau de bois feuillus. Nous avons mesuré le pourcentage de perte de poids sec pour évaluer le taux de décomposition entre les sites des ruisseaux. Les macroinvertébrés entre les sites de ruisseaux x combinaisons de source de litière de feuilles ont été identifiés à la famille, et ont été dénombrés selon leur abondance relative taxonomique, leur richesse, leur uniformité (evenness) et leur diversité. Nous n'avons trouvé aucune preuve globale d'optimisation locale de macroinvertébrés de ruisseaux en relation avec la décomposition locale de feuilles d'aulne. Les conditions locales des ruisseaux ont été le facteur le plus important qui explique la composition de communauté des macroinvertébrés dans chacun des cours d'eau, ainsi que les différences de taux de décomposition entre les ruisseaux. Nos résultats sont cohérents avec d'autres études qui ont trouvé peu de preuves d'un effet «home field advantage» pour les communautés d'organismes décomposeurs de milieux aquatiques et terrestres lorsque les deux conditions d'habitat sont similaires.

Mots clés: macroinvertébrés, fonctionnement des écosystèmes, aulne rugueux, abundance taxonomique, richesse, uniformité de Simpson, diversité de Shannon

ABSTRACT

Decomposition in freshwater streams is an ecosystem process linking riparian vegetation, the physico-chemical environment, and communities of decomposing organisms. However, the link between decomposition and diversity of the community decomposer organisms is not well understood. The objective of our study was to test the relationships between the diversity of the decomposer community and the decomposition under local conditions with respect to regional sources of dead leaves in rivers. We tested whether macroinvertebrates are locally optimized to decompose local leaf litter in comparison to regional leaf litter ("field advantage") in two small streams. In the summer of 2014, we conducted a 2 x 2 factorial pattern reciprocal field transplanting experiment with bags of speckled alder (*Alnus incana rugosa*) leaves from each of the following sources: a boreal stream and a hardwoods stream. We measured the percentage of mass loss for assessing the rate of decomposition between creek sites. The macroinvertebrates between stream sites and leaf litter source combinations were identified to the family, and were counted according to taxonomic relative abundance, richness, Simpson's evenness, and Shannon Diversity. We found global tests for local optimization of brook macroinvertebrates in relation to the local decomposition of alder leaves. Local creek conditions were the most important factor explaining the composition of the macroinvertebrate community in each stream, as well as differences in decomposition loss. Our results are consistent with other studies have found little evidence of a "home field advantage" effect for communities of aquatic and terrestrial decomposer organisms.

Key words: macroinvertebrates, ecosystem functioning, speckled alder, taxonomic abundance, richness, Simpson's evenness, Shannon Diversity

INTRODUCTION

Biogeochemical processes permit the continuous cycling of elements between organic and inorganic forms, and are thus essential to life. A key step in biogeochemical cycles is decomposition, the breakdown of dead organic matter. Decomposition is one of the most important ecosystem processes that occurs in nature as it enables the recycling of carbon and nutrients, both essential to the maintenance of primary production (Wallace et al. 1997; Gessner et al. 2010). Most herbivorous material (90%) is consumed during decomposition rather than through herbivory, making it essential to understand both terrestrial and aquatic decomposition cycles (Gessner et al. 2010). As such, decomposition is a key ecosystem function, where ecosystem functions are defined as biologically-mediated processes that determine the flow of energy and nutrients through food webs (Duffy 2002). Here, I focus on decomposition of leaf litter in small temperate streams, because in such habitats detritus is typically more important than live plant biomass in terms of supporting diverse food webs.

0.1 The link between biodiversity and ecosystem function

The causal relationship between the biodiversity of organisms and the ecosystem functions they carry out has been debated over the last two decades. Biodiversity, in this context, has often been interpreted to mean number of species but can also refer to the evenness of abundance between species, functional diversity, genotype diversity or phylogenetic diversity (Mace et al.

2013). The effect of biodiversity on ecosystem functions is of particular interest, given negative effects of human activity on community-level diversity (Murphy and Romanuk 2014); in particular, if species loss results in reduced functioning of ecosystems, then there may be a growing fragility of food webs as well as reduction in the subset of functions which are essential to the wellbeing of humans (ecosystem services: Hooper et al. 2012).

A number of studies have shown strong support for biodiversity-ecosystem function relationships, starting with the Tilman et al. (1996) common garden experiments on grassland communities that have been followed by supporting studies (Tilman et al. 1997; van der Heijden et al. 1998; Balvanera et al. 2006; Cardinale et al. 2006; Cadotte et al. 2008; Cardinale et al. 2011; Isbell et al. 2011). These studies have suggested that biodiversity is linked to species traits, which when disturbed, may change how they function in their role in the environment (i.e. disturbance regimes, microclimate, etc.; Chapin III et al. 2000; Petchey and Gaston 2006). Tilman et al. (1996) ignited a series of experiments that linked biodiversity (especially species richness: the number of species present) to ecosystem functions. In this experiment, Tilman et al. (1996) examined how having more grass species in a given plot led to more efficient use of nitrogen available in the system and higher plant productivity. Initially this and similar results were attributed to species having complementary niches (Chapin III et al. 2000). However, other researchers argued that the results could also be explained by sampling effects, because any particular species was more likely to occur in a high diversity plot than a low diversity plot, including species that are both dominant in abundance and functionally important (Loreau et al 2010). In addition, it was recognized that the species loss may disturb indirect and mutualistic interactions, indicating that species richness of a single trophic

level could not solely be used to predict how biodiversity influences ecosystem function (Zuppinger-Dingley et al. 2016).

Critiques of the biodiversity-ecosystem function studies have identified potential biases, such as a focus on simplified communities and functions, as well as on terrestrial plant communities (Schwartz et al. 2000; Duffy 2002; Srivastava and Vellend 2005; Tilman et al. 2012). Moreover, biodiversity-ecosystem function relationships may be weakened by increases in a dominant species that can act to counterbalance any decrease in species richness (Schwartz et al. 2000; Smith and Knapp 2003; Grman et al. 2010). Smith and Knapp (2003) found that when they removed rare plant species but kept the abundance consistent by adding dominant grass species individuals, the dominant grasses offset any loss of productivity (Smith and Knapp 2003). Similar results were found in a grassland study by Grman et al. (2010) over an 18-year time series experiment of disturbed and undisturbed communities. As a result of these findings, there is building evidence that biodiversity measures other than species richness may be better at predicting ecosystem functions (Wohlegermuth et al. 2016; St-Gelais et al. 2017). More recent studies are investigating biodiversity – ecosystem function relationships in trophically-complex ecosystem communities, including animals, bacteria, and fungi, to better understand the relationship between biodiversity and key ecosystem functions, such as decomposition (Lefcheck and Duffy 2015; Andrade et al. 2016; Brophy et al. 2017).

0.2 Decomposer diversity, and decomposition as a key ecosystem function in freshwater streams

In freshwater systems, decomposing organic matter supports many trophic levels of the food web, beginning with decomposers such as fungi, bacteria, and macroinvertebrates (Wallace et al. 1997; Gulis and Suberkropp 2003; Gessner et al. 2010). Among freshwater ecosystems, streams are especially influenced by a close terrestrial-aquatic interface and consequently their food webs are largely based on these terrestrial detrital sources of nutrients and carbon (Dodds and Whiles 2010). When streams are narrow with a dense riparian zone, allochthonous litter inputs are typically the dominant carbon and nutrient source for aquatic food webs (Wallace et al. 1997), although autochthonous production of algae may still be important for certain essential fatty acids (Torres-Ruiz et al. 2007). Decomposition of leaf litter in streams involves initial processes of physical leaching, followed by microbial conditioning. Following the initial colonization of the litter by bacteria and fungi, macroinvertebrates are able to further decompose leaf litter (Gulis and Suberkropp 2003). Those macroinvertebrates also support populations of larger insects or fish that feed on them, allowing nutrients to re-enter their respective cycles (e.g. carbon, phosphorus, and nitrogen) (Wallace et al. 1997; Gessner et al. 2010).

A number of studies have manipulated decomposer communities to understand how decomposer diversity affects the ecosystem function of decomposition (Hättenschwiler et al. 2005; Cardinale et al. 2006). This includes studies in both terrestrial (Scheu et al. 2002; Hättenschwiler and Gasser 2005; Grizzle and Zak 2006; Handa et al. 2014) and aquatic systems (Jonsson et al. 2001; Pascoal et al. 2005; Schädler and Brandl 2005; Balvanera et al. 2006, Cardinale et al. 2006; Srivastava et al. 2009; Handa et al. 2014).

Among the terrestrial studies, many have found support for a decomposer diversity-decomposition relationship (Scheu et al. 2002; Hättenschwiler and Gasser 2005; Grizzle and Zak 2006; Handa et al. 2014). In the aquatic environment, the relationship between decomposer diversity and decomposition has been detected in some studies but not others. For instance, decomposer diversity is positively associated with decomposition in some observational studies of streams (e.g. Jonsson et al. 2001) but not in others (Pascoal et al. 2005). Experimental manipulations of decomposer diversity have more often than not found positive effects on decomposition (meta-analyses: Balvanera et al. 2006, Cardinale et al. 2006, Srivastava et al. 2009), but there can be strong geographic differences in both the patterns and underlying mechanisms (McKie et al. 2008). Some of the differences between studies may be due to the metric of diversity used or the type of decomposer taxa considered. For example, effects of detritivore richness have been shown to differ from those of evenness (Boyero et al. 2007; McKie et al. 2008). Therefore, given the critical importance of decomposition for the ecosystem function of freshwater streams, there is a need to investigate how decomposer communities influence decomposition in streams from the perspective of both taxonomic and functional richness and evenness. Furthermore, some researchers have suggested that microbial communities have greater functional redundancy than metazoan communities, and so are less likely to show diversity-function relationships (Pascoal et al. 2005, Louca et al. 2016). Given the importance of both microbes and metazoans for leaf breakdown (Handa et al. 2014), this suggests that future research on decomposition should consider the role of the decomposer community as a whole.

0.3 Stream effects on decomposition rate: temperature and nutrients

Many different physical and chemical characteristics – most notably temperature and dissolved nutrients – can affect the decomposition rate of leaf litter in both terrestrial and aquatic ecosystems (Aerts 1997; Boyero et al. 2011; Bothwell 2014). However, the relationship between many of these characteristics and the decomposition rate is not often straightforward, since the relationships can be positive, negative, or negligible (Fierer et al. 2005; Hagan et al. 2006; Boyero et al. 2011).

Temperature can influence leaf decomposition differently, depending on whether the ecosystem is terrestrial or aquatic. Soil temperature is often positively related to the rate of decomposition (Moore 1986; McHale et al. 1998; Bothwell 2014), although this relationship is weaker at the beginning of the decomposition process, but increases with time (Fierer et al. 2005). By contrast, freshwater aquatic systems, the relationship is less clear. A number of studies have shown that increases in water temperature lead to higher rates of microbial decomposition (Dang et al. 2009; Fernandes et al. 2011; Ferreira and Chauvet 2011; Ferreira and Canhoto 2014; Ferreira et al. 2015). Past studies on macroinvertebrates have found that macroinvertebrate decomposition rates were greater at higher temperatures, potentially from increases in either the abundance of decomposers or the metabolic rate of the decomposers (Aerts 1997; Jonsson 2001; Ferreira and Canhoto 2014). For example, Ferreira and Canhoto (2014) found that temperature effects on decomposition were dependant on season: higher temperature increased decomposition in the winter but not in the summer. In this study, decomposition rate increased for

both microbial and invertebrate decomposition, although invertebrate decomposition increased more than microbial decomposition (Ferreira and Canhoto 2014). However, in a comprehensive global study by Boyero et al. (2011), an increase in microbial decomposition rate was met by a similar magnitude of decrease in macroinvertebrate decomposition rate, thereby cancelling out any overall change in decomposition. Therefore, although temperature is a strong determinant of decomposition rates, the effects of temperature are often context-dependent.

The relationship between decomposition rate and dissolved nutrients, nitrogen and phosphorus, is also complicated. Increases in phosphorus availability in lake waters have been linked with higher rates of decomposition (Xie et al. 2004). Similarly, low and moderately eutrophic streams are reported to have elevated decomposition rates compared to at pristine sites (Hagen et al. 2006). The positive influence of nutrients, especially phosphorus, on decomposition has been related to the positive effects of limiting nutrients on the abundance of decomposer populations, both macroinvertebrates (Elwood et al. 1981; Gulis et al. 2006; Hagen et al. 2006) and fungi (Gulis et al. 2006; Feio et al. 2010). However, too much of either type of nutrient can result in eutrophication that reverses positive effects of nutrients on decomposer community abundance and decomposition (Elwood et al. 1981; Gulis et al. 2006; Hagen et al. 2006; Feio et al. 2010).

Microbial decomposers are key but understudied components of the decomposer community, and can be limited by both temperature (Irons et al. 1994) and nutrient availability (Gulis et al. 2008) in streams.

For example, microbial decomposition rate has been found to moderately increase when dissolved nutrients increase during spring and summer months (Ferreira and Graça 2016). Moreover, a series of studies by Gulis and Suberkropp (2003a; 2003b) found that there was an increase of microbial biomass and decomposition rate in streams with enriched nutrients. However, comparisons between streams in agricultural versus forested settings may be poor test of the effects of nutrients because gradients in temperature, nutrients, and light can co-vary between streams (Hagen et al. 2006), and so it can be difficult to disentangle these individual effects on decomposition and decomposer communities using observational approach. Experimental approaches can help disentangle the drivers. For example, in a mesocosm experiment, when effects of nutrient enrichment were manipulated independently of other factors that often characterize agricultural streams (pesticides, sediment deposition and low flow), there was no evidence that nutrient enrichment affected or decreased the microbial decomposition rate depending on the species of leaf litter used (Bruder et al. 2016).

0.4 Leaf litter chemistry effects on stream decomposition

The nutrient availability in leaf material can influence the rate of leaf decomposition in both the terrestrial (Meentemeyer 1978; Aerts 1997; Hättenschwiler et al. 2005) and the aquatic environment (LeRoy and Marks 2006; Bruder et al. 2016; Ferreira and Graça 2016). Higher levels of nutrients (i.e. nitrogen and phosphorus) and lower levels of secondary compounds (tannins, phenolics, lignin, etc.) have been associated with higher rates of

decomposition (Aerts 1997; LeRoy and Marks 2006). For example, Ostrofsky (1997) found that using leaf tannins, nitrogen, carbon:nitrogen, and lignin explained most of variation in the macroinvertebrate decomposition rate between different tree species in streams. Others have found that leaf phosphorus concentration better predicts early decomposition, but phenolic compounds are better predictors in macroinvertebrate decomposition past the one-year mark of decomposition (Aerts and de Caluwe 1997). Differences in leaf chemistry, as a key influence on decomposition, are found not only between species, but can be observed between populations. For example, Jackrel et al. (2016) found that macroinvertebrate communities were locally optimized to decompose the local litter comprised of differences in secondary defense compounds, such as tannins, on a subspecies of red alder leaf decomposition in streams. A similar pattern has been reported for hybrids of two cottonwood species, where genotypic differences in tannin concentrations effect both aquatic and terrestrial decomposition (Schweitzer et al. 2008)

Nutrients and secondary compounds in leaf litter can be particularly important in explaining differences in litter decomposition at regional or smaller spatial scales. While climate explains much of the global pattern in the terrestrial decomposition of litter, within a climatic region, leaf litter chemistry is the best predictor of decomposition rate, especially the relationship between the secondary compound lignin and the nitrogen concentration (Meentemeyer 1978; Aerts 1997). For example, litter chemistry is a better predictor of decomposition in streams than stream condition, at least with the first month (LeRoy and Marks 2006).

Leaf litter chemistry may affect litter decomposition by determining the amount and type of litter nutrients accessible to decomposers. An important component of the decomposer community is fungi. A number of studies have elevated nutrient levels in streams and observed simultaneous increases in both decomposition and fungal biomass (Fernandes et al. 2014; Bruder et al. 2016; but see Ferreira and Graça 2016). However, there may be important differences between nitrogen and phosphorus enrichment; for example, Fernandes et al. (2014) found that increasing nitrogen but not phosphorus affected decomposition and fungi. Furthermore, nitrogen enrichment may only affect fungal communities in certain litter species, perhaps because litter species also differ in concentrations of secondary compounds that reduce nutrient accessibility (Ferreira and Graça 2016).

0.5 Decomposer community composition in relation to decomposition

Macroinvertebrates are a key component of stream decomposer communities (Gessner et al. 2010), and the taxonomic and functional community composition of stream macroinvertebrates has long been studied in relation to leaf litter decomposition in streams (Cummins and Klug 1979; Merritt and Cummins 1996). Macroinvertebrate communities themselves can be directly structured by both conditions of the water such as temperature and chemistry (LeRoy and Marks 2006; Merovich and Petty 2010), as well as physical factors such as particle size and stream width (Heino et al. 2003; Mykrä et al. 2007). However, the extent to which physico-chemical characteristics determine the community composition of stream macroinvertebrates can be highly context-dependent,

influenced both by the environmental gradient and the macroinvertebrate taxa (Heino et al. 2003; LeRoy and Marks 2006; Mykrä et al. 2007). In addition to physico-chemical stream conditions, leaf litter chemistry can also influence macroinvertebrate decomposer species richness (Yanoviak 1999) and community composition (LeRoy and Marks 2006). These findings are consistent with studies of leaf litter effects on decomposer communities in the terrestrial environment (Jewell et al. 2015, Hättenschwiler et al. 2005).

Although macroinvertebrates have historically been studied as the main agents of decomposition in streams, some studies suggest that the role of microbes has been overlooked. For example, stream conditions have been shown to affect decomposition rates in the absence of changes in the abundance of detritivorous macroinvertebrates (McKie and Malmqvist 2009, Ferreira et al. 2015), suggesting that microbial or physical breakdown of litter is also influenced by the stream environment. Often, studies have linked changes in decomposition to changes in macroinvertebrate detritivores without considering the potential for indirect effects of invertebrates on microbes (Graça 2001). However, macroinvertebrates can affect the microbial community. For example, Domingos et al. (2015) found that warming reduced the activity of a dominant macroinvertebrate decomposer (the Trichopteran, *Allogamus laureatus*) in streams, which had cascading effects on the response of the fungal community to warming. The focus on macroinvertebrate communities as the main drivers of leaf litter decomposition in streams has been replaced with more recent studies that characterize microbial components of decomposer communities (Duarte et al. 2006; Duarte et al. 2008; Duarte et al. 2009; Duarte et al. 2010). Although the taxonomic identify of microbial OTUs in decomposer communities can be ascertained by modern DNA sequencing methods, the ecological functions of

many microbial groups remain to be discovered. A promising approach here is using metagenomics to establish the relative abundances of genes, or metaproteomics to quantify the relative abundance of proteins, where these genes or proteins have known functional significance (Schneider et al. 2010; Louca et al. 2017). Findings such as these point to the ecological significance of other traditionally unexplored components of the decomposer community, namely the bacteria and fungi, and their relative importance for decomposition in streams. There remains a need to better integrate fungal and bacterial components into our understanding of stream decomposer communities, the abiotic and biotic factors that influence microbial decomposer communities, and how microbial decomposer community structure and composition influences leaf litter decomposition rates.

0.6 'Home field advantage' effects in decomposer communities

The 'Home field advantage' hypothesis predicts that local leaves should be preferred over regional leaves, regardless of chemical composition, by the decomposer community (Gholz et al. 2000). There is presently no overwhelming evidence that 'home field advantage' occurs commonly and consistently in terrestrial and aquatic decomposition (Wang et al. 2013; Veen et al. 2015b). This is because while some studies do show evidence to support 'home field advantage' effects in decomposer communities in terrestrial ecosystems (Ayres et al. 2009; Strickland et al. 2009; Wallenstein et al. 2013; Chomel et al. 2015; Veen et al. 2015a) and in freshwater streams (Jackrel and Wootton 2014; Jackrel

and Wootton 2015a; Jackrel and Wootton 2015b; Jackrel et al. 2016), many other studies have found no support for this phenomenon in nature (terrestrial studies: Gießelmann et al. 2011; St. John et al. 2011; Makkonen et al. 2012; aquatic studies: Jewell et al. 2015).

There have been several meta-analyses of the terrestrial decomposition literature that have shown both support for (Wang et al. 2013) and against (Veen et al. 2015b) 'home field advantage' effects. Wang et al. (2013) found that litter mass loss in certain forest ecosystems was significantly higher in most studies in home locations, leading to higher nitrogen releases into the environment and acceleration of nitrogen cycling. By contrast, in the meta-analysis by Veen et al. (2015b), there were varying degrees of evidence for 'home field advantage' and little linkage between either temperature or leaf litter chemical composition as drivers of 'home field advantage.' This suggests that 'home field advantage' is not ubiquitous throughout decomposition, nor are the mechanisms that cause it simple to understand.

Among terrestrial decomposition studies, there are several recent empirical papers that show inconsistencies in the level of support for 'home field advantage'. First, there are a series of papers that show no support for 'home field advantage' across a broad array of biomes globally. For example, a terrestrial reciprocal transplant involving mixes of leaf litter found no evidence of a 'home field advantage' effect in macro- and meso-invertebrate decomposition rates in the tropical rainforests of Brazil (Gießelmann et al. 2011). This finding was supported by a more comprehensive study by Makkonen et al. (2012), which preformed a reciprocal transplant of leaf litter

from 16 species in forests spanning from the subarctic to the tropics. While this study found that there were certain litter traits that predicted variation in decomposition (i.e. magnesium and condensed tannins concentrations), the decomposition rates did not vary when looking at home versus away sites, showing little specialization by the decomposer community between sites (Makkonen et al. 2012). Veen et al. (2015a) examined terrestrial decomposition in the Arctic and found limited evidence of 'home field advantage' throughout the biome. Second, there may even be evidence that `home field` effects can be disadvantageous rather than advantageous. St. John et al. (2011) addressed differences in decomposition rate between microinvertebrate and microbial decomposers in New Zealand found that decomposition rate was slower rather than faster at home sites compared to away sites (St. John et al. 2011). Thirdly, some studies show evidence for mixed support for 'home field advantage' that depends on leaf litter species and whether mono-species or mixed-species leaf litter types were considered. Chomel et al. (2015) detected mixed evidence for 'home field advantage' effects with spruce and poplar litter decomposition in the boreal region of Québec, Canada. Only the spruce litter had a faster decomposition rate at home sites compared to away sites, but also exhibited higher abundance of decomposers as compared to the poplar litter (Chomel et al. 2015). Jewell et al. (2015) provided further insight into understanding mixed support for 'home field advantage' between terrestrial decomposition studies: effects are much stronger when looking at mono-specific litter than litter mixed together.

Among terrestrial decomposition studies, there are also several recent papers that have found positive support for 'home field advantage' effects. In a terrestrial microcosm experiment that crossed the origin of soil microbial

communities with the origin of leaf litter (tree leaf litter versus grass litter), tree leaf litter decomposed more rapidly when exposed to home microbial communities but grass leaf litter was decomposed effectively by all microbial communities (Strickland et al. 2009). The authors suggest that microbial community under poor quality litter are filtered or selected to contain only those species able to persist on low quality litter, but not those under high quality litter (Strickland et al. 2009). A similar mechanism has been suggested to explain why lodgepole pine, a recalcitrant litter, benefits more from a home field advantage than aspen, a more labile litter (Wallenstein et al. 2013). Therefore, while many terrestrial decomposition studies have not found support for 'home field advantage', we cannot ignore that these effects do occur in certain study systems and under certain conditions in terrestrial ecosystems. More research is needed to understand the conditions under which 'home field advantage' effects do and do not occur in nature.

Less research has been done to test for `home field advantage effects` in aquatic ecosystem decomposition compared to in terrestrial ecosystem decomposition. Even reviews of the home field advantage literature have been unable to include any aquatic studies (Wang et al. 2013; Veen et al. 2015b). In fact, the only studies to our knowledge to examine home field advantage in an aquatic system are recent and all based in Washington State, USA. This series of studies found evidence of 'home field advantage' in the decomposition of red alder (*Alnus rubra*) and Western Hemlock (*Tsuga heterophylla*) litter, as well as in subspecies of red alder (Jackrel and Wootton 2014; Jackrel and Wootton 2015b; Jackrel et al. 2016). However, when they looked at other species (i.e. big leaf and vine maple), they did not see any differences in decomposition rate, despite intraspecific variation in chemical composition (Jackrel and Wootton 2015).

These results from streams contrast with many terrestrial studies in that the macroinvertebrates were explicitly included in the decomposer community, and that home field advantages were shown both for recalcitrant (Western Hemlock) and labile (red alder) litter. In the case of the intraspecific home field advantage, the authors suggest that the stream macroinvertebrate communities are specialized to the particular defensive chemical make up of their local alder population (Jackrel et al. 2016). For example, subspecies of red alder have varying degrees of defensive secondary chemicals, such as tannins (Jackrel and Wootton 2014; Jackrel et al. 2016). In summary, 'home field advantage' effects in stream decomposer communities may be limited to certain litter species, and could potentially be dependent on the community composition of riparian vegetation.

0.7 Objective of my thesis

Given mixed support for 'home field advantage' effects in the global terrestrial decomposition literature and the paucity of studies that have addressed this potential ecological mechanism in aquatic ecosystems, my thesis tested for 'home field advantage' effects in macroinvertebrate decomposer communities between two freshwater streams, one in the boreal forest and one in the deciduous forest, in Québec, Canada. I performed a reciprocal transplant experiment with speckled alder (*Alnus incana rugosa*) collected from each of the two biomes, and then examined relationships between leaf litter decomposition rate and taxonomic and functional macroinvertebrate community structure and

composition as a response to the effect of stream, leaf litter source, and stream x leaf litter source interactions. I also characterized the microbial decomposer community present in the two streams on leaf litter sources originating from the two different biomes.

The rationale for positive support of the 'home field advantage' hypothesis in my experiment was based on three principal assumptions: i) leaf litter quality would differ between the alder collection sites in the two forest biomes, ii) differences in leaf litter quality between the two forest biomes would result in differences in the stream community assemblages of macroinvertebrates, and possibly also fungi and bacteria, and iii) differences in community assemblages of macroinvertebrates on different leaf litter sources would result in `home field` effects when measured as decomposition rates within each of the streams.

There were three alternative predictions associated with testing the 'home field advantage' hypothesis in my study:

1) H_0: There will be no correlation between speckled alder leaf decomposition rate and any of taxonomic diversity, richness, and evenness of stream macroinvertebrate communities. A possible mechanism to explain this hypothesis is if stream abiotic effects have overriding effects on decomposition rates and macroinvertebrate communities.

2) H_1: Macroinvertebrate community diversity, richness, and evenness will correlate with speckled alder decomposition rate, but independently of leaf litter source. If this is the case, there will not be evidence to support 'home field advantage', but there will be evidence to support the

importance of macroinvertebrate community properties on stream leaf litter decomposition.

3) H_2: Macroinvertebrate community diversity, richness, and evenness will positively correlate with speckled alder decomposition rate depending on leaf litter origin (home forest biome versus away forest biome). If this is the case, there will be support for the 'home field advantage' hypothesis because local leaf litter will decompose more rapidly with local macroinvertebrate community assemblages compared to regionally distant source macroinvertebrate community assemblages.

CHAPTER I

DIVERSITY MEETS DECOMPOSITION IN FRESHWATER STREAMS: TESTING FOR A 'HOME FIELD ADVANTAGE' IN FRESHWATER DECOMPOSER COMMUNITIES IN A BOREAL VERSUS A TEMPERATE HARDWOOD STREAM

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1.1 Abstract

The link between ecosystem function and biodiversity has been hotly debated in the past, as this relationship is not well understood. This relationship is often complicated and frequently dependent on local factors and regional differences. Decomposition – an essential ecosystem process – is responsible for the recycling of nutrients and bridging aquatic and terrestrial ecosystems. Our study examined if macroinvertebrates are locally optimized to decompose local leaf litter over regional ('home field advantage'). Using speckled alder (*Alnus incana rugosa*), we performed a reciprocal transplant between two streams in two different biomes. We measured percent dry mass loss to estimate decomposition and identified macroinvertebrates to family level. Using the macroinvertebrate data, we determined taxonomic abundance, richness, evenness, and diversity. We did not find any evidence for 'home field advantage' in either the leaf decomposition or in biodiversity of the macroinvertebrate community. However, both diversity and evenness were positively correlated with decomposition, with the highest diversity, evenness, and decomposition occurring in the hardwoods stream. As our model selection showed that both diversity and stream location correlated with decomposition, we caution that these results may not be definitive, making it difficult to determine relative effects. These results are consistent with a number of other studies that have found little evidence of 'home field advantage' in decomposer communities, while supporting that there is a positive relationship between ecosystem function and biodiversity.

Key Words: macroinvertebrates, ecosystem function, speckled alder, taxonomic abundance, richness, Simpson's Evenness, Shannon Diversity

1.2 Introduction

The link between biodiversity and ecosystem function is a cornerstone principle in ecology because it underlies our understanding of ecological processes and how they may be conserved in face of environmental change (Tilman et al. 1996; Wardle et al. 1997; Schwartz et al. 2000; Duffy 2002; Hooper et al. 2005; Srivastava and Vellend 2005; Tilman et al. 2012; Tobner et al. 2014; etc.). Decomposition is a key ecosystem function that enables nutrient cycling and basal resources for higher trophic levels (Taylor et al. 2007; Roussel et al. 2008; Gessner et al. 2010; Milcu and Manning 2011). Many studies have debated the relationship between species biodiversity and ecosystem function (Schwartz et al. 2000; Duffy 2002; Smith and Knapp 2003; Srivastava and Vellend 2005; Roussel et al. 2008; Grman et al. 2010; Tilman et al. 2012), and the link between species biodiversity and decomposition is also unclear. While some studies have found no link or mixed outcomes between species taxonomic biodiversity and decomposition (Hättenschwiler and Gasser 2005; Pascoal et al. 2005; Schädler and Brandl 2005; Srivastava et al. 2009), other key works on decomposition have shown support for biodiversity-ecosystem function relationships (Balvanera et al. 2006; Handa et al. 2014). One factor that may enhance or inhibit relationships between decomposer diversity and decomposition are 'home field advantage' effects. The 'home field advantage' hypothesis (Gholz et al. 2000) is based on the idea that organic material will decompose faster in an area where the material has originated from, regardless of quality due to specialization by local decomposer communities to local conditions (Gholz et al. 2000; Schweitzner et al. 2004; Lecerf and Chauvet 2008, O'Brien and Krauss 2010; Makkonen et al. 2012; Jewell et al. 2015).

'Home field advantage' implies that one or several species within all or some functional or taxonomic groups are locally optimized to local leaf litter and this specialization overcomes other variables, such as temperature and leaf litter quality (Schweitzer et al. 2004; Makkonen et al. 2012; Jewell et al. 2015; Powell et al. 2015; Veen et al. 2015a, Veen et al. 2015b). Austin et al. (2014) propose that 'home field advantage' takes place when a local community is optimized to perform its function due to the complex interaction of surrounding conditions (i.e. temperature, nutrient availability, leaf litter chemical composition, pH, dissolved oxygen, etc.). The goal of our study was to test if 'home field advantage' effects are present in decomposer communities, and how these effects may potentially influence the relationship between decomposer community diversity and decomposition in freshwater streams.

The 'home field advantage' hypothesis has been tested in terrestrial and aquatic decomposition studies, where it has met mixed support (Schweitzer et al. 2004; Chapman and Koch 2007; Ayres et al. 2009; Chomel et al. 2015; Jewell et al. 2015; Veen et al. 2015a; Veen et al. 2015b). This is because local characteristics known to influence decomposition rate, such as temperature and leaf litter chemical composition, may not solely determine the presence and strength of 'home field advantage' effects in decomposer communities (Wallenstein et al. 2013; Austin et al. 2014; Powell et al. 2015; Veen et al. 2015b). There has been little to no support for 'home field advantage' effects at large scales (Makkonen et al. 2012; Veen et al. 2015a). When 'home field advantage' effects do appear to play out in decomposer communities, it can occur at smaller spatial scales. For example, 'home field advantage' effects in aquatic decomposition studies have been recorded among local sites where there are differences in the chemical

composition of leaves as a result of plant defense responses to predation damage from insects (Jackrel and Wootten 2014; Jackrel et al. 2016). Despite that there are clear differences in quality, leaves are still decomposed quicker in their local or 'home' environment (Strickland et al. 2009; Jackrel and Wootten 2014; Jackrel et al. 2016). In a common garden experiment by Strickland et al. (2009), they found that litter quality could not solely predict how communities would respond to leaf litter, with some preferring their local litter source. However, few studies have tested for 'home field advantage' effects between biomes at a regional scale to see if these specializations to local conditions are ubiquitous in different ecosystems (Jackrel and Wootten 2014; Veen et al. 2015a; Jackrel et al. 2016).

Among the studies that have tested for regional effects, most have used different species of leaf litter that fulfill similar roles within the ecosystem or have used one common source of litter rather than a reciprocal transplant (Boyero et al. 2011). 'Home field advantage' in decomposition has been most prevalent in leaf litter decomposition studies that have used one species of leaf litter instead of a multi-species mixture, likely because of cancelling effects between leaf litter types that may occur in decomposer communities, regardless of what the leaf litter quality was recorded as (Chomel et al. 2015; Jewell et al. 2015; Veen et al. 2015b). In general, intraspecific trait variation within a single species is increasingly recognized to have an important role in community ecology (Bolnick et al. 2011; Violle et al. 2012). One of these important roles may be in how intraspecific leaf litter traits mediate 'home field advantage' effects in decomposer communities, such as differences between cottonwood subspecies leaf litter (cottonwood: LeRoy and Marks 2006; red alder: Jackrel and Wootton 2014; Jackrel and Wootton 2015; Jackrel et al. 2016).

However, it has been difficult to determine which intraspecific traits may be causing 'home field advantage' effects. For example, intraspecific differences in nutrient and secondary compound concentration of leaves have played an important role in determining a 'home field advantage' in some systems (cottonwood: Jackrel and Wootton 2014; Jackrel et al. 2016), but not others (subarctic tundra: Veen et al. 2015b). These different findings between studies and study systems highlight the need for more research on a variety of different ecosystems to gain a clearer understanding of the mechanisms governing 'home field advantage', and how it can influence biodiversity-ecosystem function relationships.

In freshwater decomposer communities, macroinvertebrates and the microbial community – composed of fungi and bacteria – are responsible for the chemical breakdown and recycling of the litter (Hynes 1970; Cummins 1973; Cummins and Kluns 1979; Graça et al. 2001; Gessner et al. 2010). Both groups have a closely linked relationship with one another: the microbial community helps to start the chemical breakdown while a number of macroinvertebrate families physically shred the leaves, further facilitating microbial breakdown of leaf litter (Hynes 1970; Cummins 1973; Cummins and Kluns 1979; Graça 2001; Gessner et al. 2010). The macroinvertebrates have a diversity of functional roles in leaf litter decomposition, including predators (who eat other macroinvertebrates), grazers-scrapers (feed on the biofilm covering leaves), collectors (gather fine particulate organic matter), and shredders (coarse particulate organic matter; Hynes 1970; Cummins and Kluns 1979; Graça 2001; Gessner et al 2010). Since taxonomic and functional groups of macroinvertebrates can respond to both leaf litter as a decomposition substrate as well as to local environmental factors in streams, it is important to tease out the direct and indirect influences of these

local effects in understanding the potential presence and strength of 'home field advantage' effects in decomposer communities. Moreover, the composition and structure of decomposer communities can differ among habitats depending on regional influences such as biogeography (Hynes 1970; Gessner et al. 2010). Therefore, both local and regional differences among habitats can potentially disrupt relationships between decomposer community diversity and decomposition when decomposer communities are not matched with their source decomposition substrate ('home field advantage'; Powell et al. 2015; Veen et al. 2015a; Veen et al. 2015b).

The objective of our study was to test for relationships between macroinvertebrate decomposer community diversity and decomposition under conditions of local versus regional sources of intraspecific leaf litter in freshwater streams. In the case of a 'home field advantage' – which predicts that local decomposer communities were optimized in terms of decomposition rate on local source leaf litter – we predicted that a relationship between macroinvertebrate decomposer diversity and decomposition between streams would be strongest.

Under this scenario, the biodiversity-ecosystem function relationship would be strongest for local decomposer communities on local source leaf litter and weakest for local decomposer communities on regional source leaf litter (Fig. 1.1a). Alternatively, if there is no home field advantage for decomposer communities on local source leaf litter, then we anticipated that biodiversity-decomposer relationships would be driven by between-stream differences in

macroinvertebrate community composition and family dominance (family evenness) rather than differences in leaf litter source (Fig. 1.1b, c).

Our study has a broader significance for biodiversity and ecosystem function relationships in a changing global environment because 'home field advantage' effects in decomposer communities have potential to limit the efficacy of decomposition in freshwater streams at regional scales as riparian plant species and populations shift northwards in response to a warming climate (Chen et al. 2011; Veen et al. 2015a)

a) Biodiversity-decomposition relationships when a 'home field advantage' is present in the decomposer community

b) Biodiversity-decomposition relationships when a 'home field advantage' is not present in the decomposer community, and biodiversity is related to decomposition

c) Biodiversity-decomposition relationships when a 'home field advantage' is not present in the decomposer community, and biodiversity is not related to decomposition

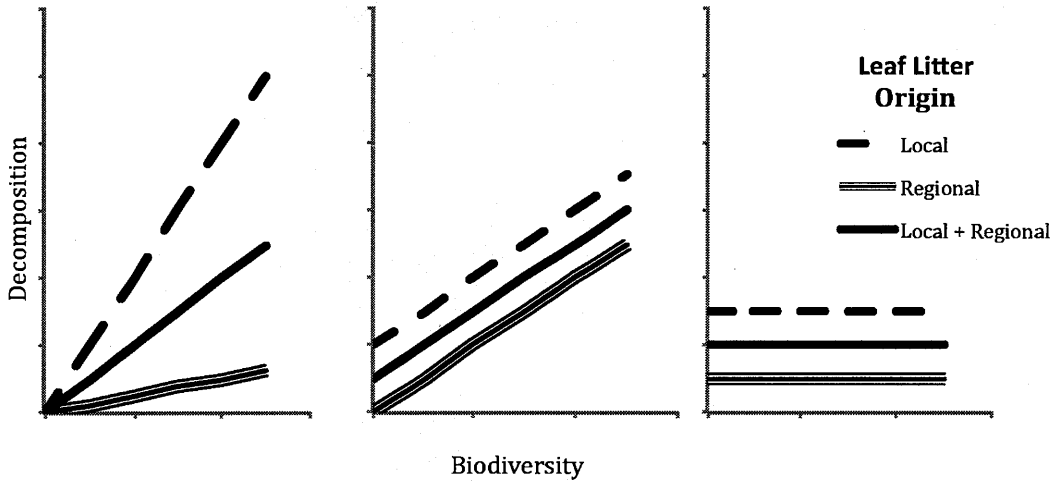

Fig. 1.1 Conceptual diagram of thesis hypotheses that predict the relationship between biodiversity and decomposition: a) if there is a 'home field advantage' for the decomposer community, then a biodiversity-decomposition relationship will be apparent across leaf source types, but will be most pronounced on local source leaf litter compared to non-local source leaf litter versus if there is no 'home field advantage' for the decomposer community, then there b) may or c) may not be a relationship between biodiversity and decomposition but there will be no difference in the biodiversity-decomposition function between local versus regional source leaves.

1.3 Methods

We conducted a reciprocal transplant field experiment involving local and regional sources of a single species of alder (speckled alder: *Alnus incana rugosa*), a common riparian shrub (Fryer 2011), in leaf litter bags placed in a freshwater stream in each of two regional biomes (temperate hardwood versus boreal) in Québec, Canada (Fig. 1.2). The experiment was a 2 x 2 factorial design with study stream and alder leaf litter source from each of two biomes (temperate hardwood forest and boreal forest) as main effects. Alder leaf sources were reciprocally exchanged between the two biomes in the streams where local macroinvertebrate communities were allowed to colonize the leaf bags (Fig. 1.2). Leaf collection took place in early July 2014, followed by a 7-week incubation of the leaf bags in the streams from mid-July to late August 2014. The leaf bags were incubated in the streams in summer rather than in autumn to minimize between-stream physical differences in temperature and photoperiod during the interval of the experiment. We did this to maximize the opportunity to detect 'home field advantage' effects in local decomposer communities that were potentially related to differences between local and regional sources of leaf litter rather than regional differences in seasonality.

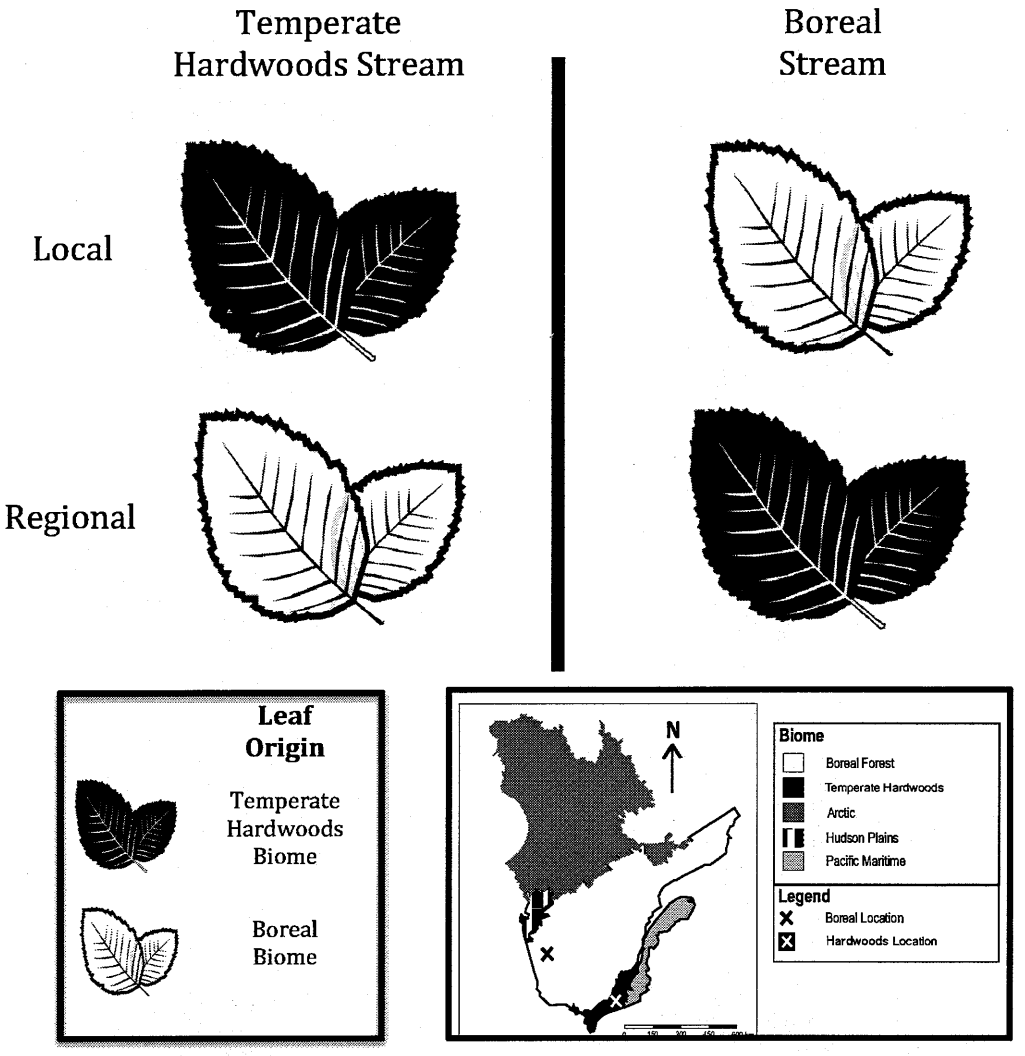

Fig. 1.2 Schematic of regional-scale reciprocal transplant of speckled alder (*Alnus incana rugosa*) in a boreal stream and a temperate hardwoods stream in Québec, Canada

1.3.1 Study streams

The two study streams were West Creek, located within the temperate hardwood forest biome (Gault Nature Reserve, Mt. St. Hilaire: 45°32'41.50"N, 73° 9'25.80"W) and Ruisseau des Peureux in the boreal forest biome (Parc Aiguebelle, Abitibi: 48°26'58.82"N, 78°47'15.32"W) (Fig. 1.2). Both study streams are pristine and located within nature reserves. Physico-chemical characteristics of each stream were measured at the beginning and at the end of the experiment. The % foliage cover and the % composition of bottom substrate were estimated visually. The bank width and water depth for all leaf litter bags was measured and averaged at each stream. Water velocity was calculated using a FlowTracker Handheld ADV flow meter (SonTek, San Diego, CA, USA). Water temperature was measured every hour for the duration of the seven-week experiment with two HOBO Water Temperature Pro v2 data loggers (Onset, Bourne, MA, USA) per stream that were attached to randomly selected leaf litter bags. Salinity, pH, conductivity, and specific conductivity were measured with a YSI Professional Plus Mulitparameter Water Quality Instrument (YSI Incorporated, Yellow Springs, OH, USA) at the beginning and end of the experiment for each experiment. Water samples were collected at the beginning and end of the experiment and analyzed for dissolved organic carbon (DOC; between 2-3 replicates), total nitrogen (TN; between 2-3 replicates), total phosphorus (TP; between 1-3 replicates), chlorophyll *a* (chl*a*; between 1-2 replicates), and bacterial production (BP; 3 replicates), and refrigerated until analyses.

The DOC concentration for each stream was measured using water samples filtered through 0.45 μm filters (surfactant-free membrane filters) after acidification (5% phosphoric acid) followed by sodium persulphate oxidation using a 1010 TOC analyser (O.I. Analytical, College Station, TX, USA). TP was quantified by spectrophotometry using a 2-cm quartz cuvette in a BiochromUltrospec® 20100 pro spectrofluorometer using the molybdenum blue method after persulphate digestion (Griesbach and Peters 1991). TN samples were analyzed using a continuous flow analyzer (ALPKEM Flow Solution IV©) using an alkaline persulfate digestion method with a cadmium reactor, following a standard protocol by Patton and Kryskalla (2003). Chl*a* was measured by filtering water using glass fibre filters (Whatman GF/F), then extracting the chl *a* in hot ethanol and measuring the chlorophyll spectrophotometrically on a BiochromUltrospec® 2100 pro with a 10-cm quartz cuvette (Winterman and de Mots 1965; Sartory and Grobelaar 1984). Bacterial production in each stream was estimated by measuring the rates of protein synthesis with radiolabelled leucine at the end of the experiment (Smith and Azam 1992; Kirchman and Ducklow 1993). These samples were incubated with ^{14}C-leucine for one hour at ambient water temperature. Incubation was stopped by adding 100% trichloroaceticacid (TCA), then stored at 4°C. Samples were then counted in a Packard Tri Carb Liquid Scintillation Analyser, model 2800 TR (Perkin Elmer, Waltham, MA, USA).

1.3.2 Leaf sources

Speckled alder leaf litter was collected in the temperate hardwood forest biome from Hudson, Québec (45°26'19.26"N, 74° 8'28.68"W and in the boreal forest biome from Abitibi, Québec (Lac Duparquet Field Station:48°31'9.91"N, 79°22'45.52"W) (Figure 1.2). The leaves were removed from the tree at different heights, with a preference for older leaves that were identified as being darker in colour, and refrigerated until they were processed.

In the laboratory, leaves were dried at 40°C for ~24 hour, then separated into sections that weighed approximately 3 ± 0.03 g, and then packaged into 24 cm x 20 cm leaf bags. For each stream, half of the leaf bags (12 per stream) contained local source leaves and the other half contained regional source leaves from the other biome (12 per stream). To tease out the relative influence of macroinvertebrates in relation to the total decomposer community that also includes bacteria and fungi on alder leaf decomposition, we used two sizes of mesh for the leaf bags: fine mesh (0.25 mm^2; 12 bags/stream, 6 of each litter source) and coarse mesh (1 cm^2; 12 bags/stream, 6 of each litter source). The bags were individually anchored to the bottom of the stream using aluminum metal pegs attached by zip-ties along with a few rocks on top of the peg to keep it in place. Bags were placed in the centre of the stream in riffles, exposed to natural elements (i.e. changes in current, light travelled through the canopy). While the coarse mesh bags allowed for decomposition by both macroinvertebrate and microbial decomposers, the fine mesh bags excluded macroinvertebrates from aiding in decomposition (Graça et al. 2005). One coarse leaf litter bags was lost during the experiment and another coarse leaf

litter bag was removed too early during the experiment, both from the hardwoods stream and each of a different leaf litter source. The leaf bags were gently rewetted with deionized water to reduce breaking during transportation to the streams. The filled leaf bags were refrigerated until their deployment into the streams.

Within each of the two streams, the leaf bags were placed in a randomized pattern. On day 0, half of all of the leaf bags were removed to account for handling loss. With the exception of two leaf bags that were lost at the temperate hardwood forest stream (one coarse-mesh bag with boreal leaves from the boreal biome and one coarse-mesh bag with temperate hardwood leaves from the temperate hardwood biome), all leaf bags were successfully retrieved during the final collection on week 7. As soon as the leaf bags were collected, they were frozen at -20°C until they could be dried and weighed.

We measured leaf characteristics from both leaf source locations at the beginning of the experiment that could potentially explain the presence or absence of a home field advantage in the decomposer community: leaf toughness, hemicellulose, cellulose, and lignin concentration. Leaf toughness was used as a proxy for differences in leaf conditions, and was determined using a 1.5mm needle. Ten leaves from each leaf collection site were tested, and each leaf was tested five times. Each leaf was penetrated with a needle attached to a pressure gage to determine how much pressure needed to be applied to break through the leaf. Lignin, hemicellulose, and cellulose concentration were measured using a fiber analyzer (Ankom2000, Ankom Macedon, NJ, USA) and following the methodology outlined by Ryan et al. (1990). These leaf

characteristics were compared between the two regional leaf sources in summer 2014.

1.3.3 Ecosystem function: decomposition rate

Following removal of macroinvertebrates and the rinsing of the leaves using deionized water in a sieve, we stored the leaves at -20°C in order to subsequently calculate the amount of leaf decomposition in the leaf bags. Leaves from each leaf bag were re-dried at 105°C for ~24 hour and then weighed to the nearest 0.01 g. The decomposition loss was determined through calculation of % mass leaf loss with the following equation: % leaf mass loss $= \frac{\text{End Dry Mass}}{\text{Start Dry Mass}} \cdot 100$.

1.3.4 Macroinvertebrate decomposers

Macroinvertebrate community composition and diversity in the leaf bags were quantified in the laboratory at UQAM. On day 0 for the initial leaf bags and on week 7 for the final leaf bags, the leaves were removed from leaf bags and rinsed with double-distilled ionized water. The macroinvertebrates were collected on a 500µm sieve and preserved in 95% ethanol. We used a 10x-dissecting microscope (SZ2-IL-ST, Olympus SZ, Japan) that was equipped with a DP21-HS Olympus camera (Olympus, Japan) to identify macroinvertebrates to family using the identification key in Marshall (2006). We enumerated the relative

abundance of each macroinvertebrate taxonomic order and family in each leaf bag (number of individuals per bag). Shannon's Diversity, local taxon richness (α-diversity), and Simpson's Evenness metrics were calculated for the total macroinvertebrate community and for each taxonomic order in each leaf bag for both sizes of leaf litter bags. Shannon's Diversity and Simpson's Evenness were calculated using EstimateS Version 9.1.0 software (Colwell 2013). Biodiversity measures were not calculated for the order Trichoptera because the trichopteran larvae were too small to identify below order, so Trichoptera were excluded from these analyses.

1.3.5 Statistical analyses

Differences in decomposition rate between streams and between leaf litter sources was analyzed as percent leaf mass loss (dry mass) in each of the coarse-mesh and the fine-mesh leaf bags by PERMANOVA in Primer6 v. 6.1.11 (PRIMER-E Ltd, Lutton, United Kingdom). Differences in leaf quality between regional sources in summer, and comparisons within sources between summer and fall were compared with Student t-tests. Simple linear regression was employed to detect relationships between macroinvertebrate diversity metrics and decomposition rate (% dry leaf mass loss). For total macroivertebrate regressions in which local and regional leaf sources were combined, Shannon Diversity was transformed using $\sqrt{2 - \text{Shannon Diversity}}$ to achieve a normal distribution. This inverted our data, making higher Shannon Diversity on the left of the x-axis, instead of on the right. We considered family diversity both of the entire assemblage, as well as within orders. Although some orders, notably

Odonata, are predators rather than detritivores, they may indirectly control decomposition through top-down effects on detritivores. Regressions were performed using e1071 (Meyer et al. 2015) and MASS (Venables and Ripley 2002) packages in R (R Core Team 2015).

As we had a number of *a priori* hypotheses about the main determinants of decomposition, we used a model selection approach. Here we compared models based simply on stream, or litter origin, or their interaction with models based on diversity (Shannon, alpha and evenness) of either the total assemblage or just Ephemeoptera. We also included a null model with no explanatory terms. The top model was selected based on AICc, and all models within 2 AICc units of this top model were considered in the plausible set. Model selection employed the MuMin R package (Bartoń 2015) on GLMs with a gamma distribution.

To distinguish treatment effects on overall macroinvertebrate community composition, we performed non-metric multidimensional scaling (NMDS) with the vegan function (Okensen et al. 2016) in R (R Core Team 2015). We analyzed variation in macroinvertebrate community metrics of Shannon Diversity, α - diversity, and Simpson's Evenness among treatment combinations by PERMANOVA with Primer6 v. 6.1.11 (PRIMER-E Ltd, Lutton, United Kingdom). Our data was non-normal, despite efforts to transform it, so we used type III permutational multivariate analysis of variance (PERMANOVA) with 999 permutations of residuals to create distribution-free data (Anderson et al. 2008) and calculated a pseudo-F that is equivalent to the F statistic produced using ANOVA (Anderson 2001). Significant terms were further analyzed using *a posteriori* pairwise comparison ($P < 0.05$). All abundance data were transformed using a log (x+2) transformation.

All data for α-diversity PERMANOVAs were fourth-root transformed to achieve normal distributions. Significant differences were detected at $P < 0.05$.

1.4 Results

1.4.1 Characterization of study streams and leaf sources

The two study streams were similar with regards to substrate, flow rate, width, depth, summer temperature, pH, and % foliage cover over the interval of our experiment (Table 1.1). However, the temperate hardwood stream had higher nutrient but lower DOC concentrations compared to the boreal stream (Table 1.1). The temperate hardwood stream also hosted a higher level of bacterial production (Table 1.1).

We verified that leaf quality differed between regional alder leaf sources during the summer. Although there was also no difference between leaf toughness (boreal = 8.2 ± 3.6 cm, temperate hardwood = 6.2 ± 2.4; Student t-test: $t_9 = 2.19$, $P = 0.056$) and cellulose levels ($t_4 = 0.16$, $P = 0.882$; Table 1.2; Fig. 1.3) between the boreal and temperate hardwood leaves, hemicellulose was higher in the boreal leaves compared to the temperate hardwood leaves ($t_4 = 10.92$, $P = 0.004$; Table 1.2; Fig. 1.3). By contrast, the lignin levels were lower in the boreal leaves

compared to the temperate hardwood leaves (t_4 = 22.83, P = 0.001; Table 1.2; Fig. 1.3).

Table 1.1. Summary of physical and chemical characteristics of two streams used in a reciprocal leaf transplant from summer 2014 at the start and end of a 7-week experiment. Values are mean ± SD; * signifies a single measurement.

Test	Temperate hardwood Stream		Boreal Stream	
	Start (July 10 2014)	End (August 26 2014)	Start (July 14 2014)	End (September 2 2014)
Average Daily Water Temperature (°C)	13.27 ± 1.24		14.87 ± 1.35	
Stream Width (m)*	3.0	1.64	2.3	2.3
Average Stream Depth (cm)	7.22 ± 2.29	3.55 ± 1.09	15.02 ± 3.67	8.50 ± 2.25
Total Phosphorus (µg/L)	12.45 ± 1.69	18.59 ± 1.90	5.86 ± 2.54	6.53 ± 1.44
Total Nitrogen (mg/L)	0.198 ± 0.020	0.195 ± 0.003	0.144 ± 0.001	0.207 ± 0.014
Dissolved Organic Carbon (mg/L)	0.898 ± 0.074	0.242 ± 0.081	6.33*	4.874 ± 0.162
Chlorophyll *a* (µg/L)	0.3068*	0.4339 ± 0.0542	0.2109 ± 0.00	0.3068 ± 0.2712
Bacterial Production (µC $L^{-1}day^{-1}$)	-	32 282 ± 6264	-	24 955 ± 8545
pH*	8.15	7.25	7.4	6.71
% Foliage cover*	65	80	60	85
Conductivity (µS/cm)*	80	146.6	31.1	90.71.
Flow Rate (m^3/s)	0.021 ± 0.003	0.107 ± 0.013	0.049 ± 0.001	0.006 ± 0.004

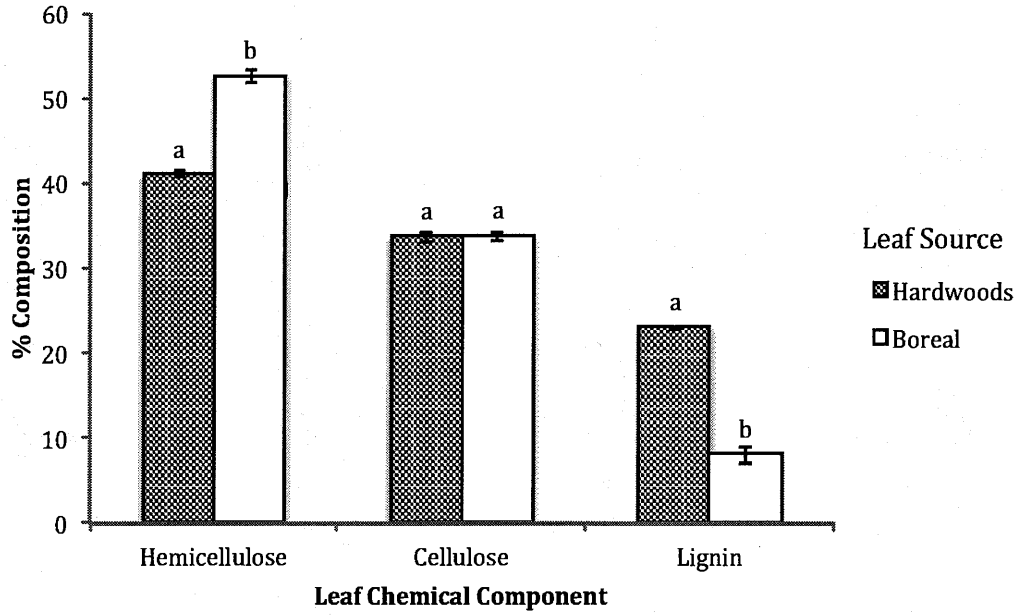

Fig. 1.3 A comparison of summer speckled alder (*Alnus incana rugosa*) leaf chemistry from leaves collected between regional sources (hardwoods (n = 3) versus boreal (n = 3) biomes) for the reciprocal transplant experiment: % hemicellulose; % cellulose; and, % lignin. Letters indicate significance between biomes ($P<0.05$).

Table 1.2. Mean ± SD percentage composition of leaf chemistry used in reciprocal transplant.

Leaf Source	% Hemicellulose	% Cellulose	% Lignin
Hardwoods	40.1 ± 0.4	33.7 ± 0.6	23.0 ± 0.2
Boreal	52.6 ± 0.9	33.8 ± 0.5	8.0 ± 1.1

1.4.2 Ecosystem function: decomposition rate

Stream but not leaf source affected decomposition rate: percent mass leaf loss was higher in the temperate hardwood forest stream than in the boreal stream in the coarse-mesh bags where decomposition occurred through the action of both macroinvertebrates and microbial decomposers (Table 1.3; Fig. 1.4a). Macroinvertebrates appeard to play a significant role in the decomposition of the leaf litter in the coarse-mesh bags as there was no difference in decomposition rate between streams or leaf sources in the fine mesh bags where macroinvertebrates were generally excluded (Table 1.3; Fig. 1.4b).

1.4.3 Macroinvertebrate community diversity – decomposition relationships

While macroinvertebrates were present in fine mesh bags, they were relatively limited (Table A. 1). Macroinvertebrates that composed the decomposer community belonged to six orders and a minimum of 15 families (due to being unable to identify the Trichoptera, the total number of families is unknown), including a single Coleoptera (family Eulichadidae) individual belonging to a litter bag in the hardwood streams (Table A.2). The hardwood stream contained at least seven families while the boreal stream had 13 families including eight families of Ephemeroptera unique to this stream. There were four families in common between the two streams (Table A.2).

For the total macroinvertebrate community, there were relationships between diversity measures (Shannon Diversity, α-diversity, and Simpson's Evenness) and decomposition rate (percent leaf mass loss) when local and regional leaf sources were combined in the regressions (Tables 1.4-1.7; Fig. 1.5 a-c). We found a negative relationship between taxon richness and decomposition, but a positive relationship between taxon Shannon diversity and decomposition and taxon evenness and decomposition (Fig. 1.5). However, there was no evidence to support a 'home field advantage' for the total macroinvertebrate community because diversity-decomposition relationships on local and regional source leaves were not significant when considered separately. We did observe that local leaf litter decomposition was significant correlated to taxon Shannon diversity, taxon diversity, and taxon evenness we looking at Ephemeroptera (Fig. 1.5).

Table 1.3 Results for % mass loss from leaf litter bags that allow for both macroinvertebrate and microbial decomposition and bags that only allow for microbial decomposition. Results are from a PERMANOVA with stream location and leaf source as fixed effects under 999 permutations.

	Macroinvertebrate + Microbial (Coarse Mesh) % Mass Loss	Microbial (Fine Mesh) % Mass Loss
d.f. effect	1	1
d.f. total	6	8
Stream Location		
mean ± SD		
Hardwoods	96.14 ± 6.65	61.06 ± 12.28
Boreal	65 ± 7.76	57.38 ± 10.08
Pseudo-F	10.094	0.237
P(perm)	**0.016**	0.645
Leaf Source		
mean ± SD		
Hardwoods	81.36 ± 16.88	62.10 ± 8.39
Boreal	74.47 ± 18.64	56.34 ± 12.52
Pseudo-F	2.6172	0.875
P(perm)	0.136	0.378

SL x LS

mean ± SD		
Hard. x Hard.	99.16 ± 1.19	64.24 ± 5.23
Hard. x Boreal	93.12 ± 9.73	57.89 ± 17.79
Boreal x Hard.	69.49 ± 6.42	59.95 ± 11.47
Boreal x Boreal	62.03 ± 8.23	54.80 ± 8.27
Pseudo-F	0.2613	0.070
P(perm)	0.633	0.825

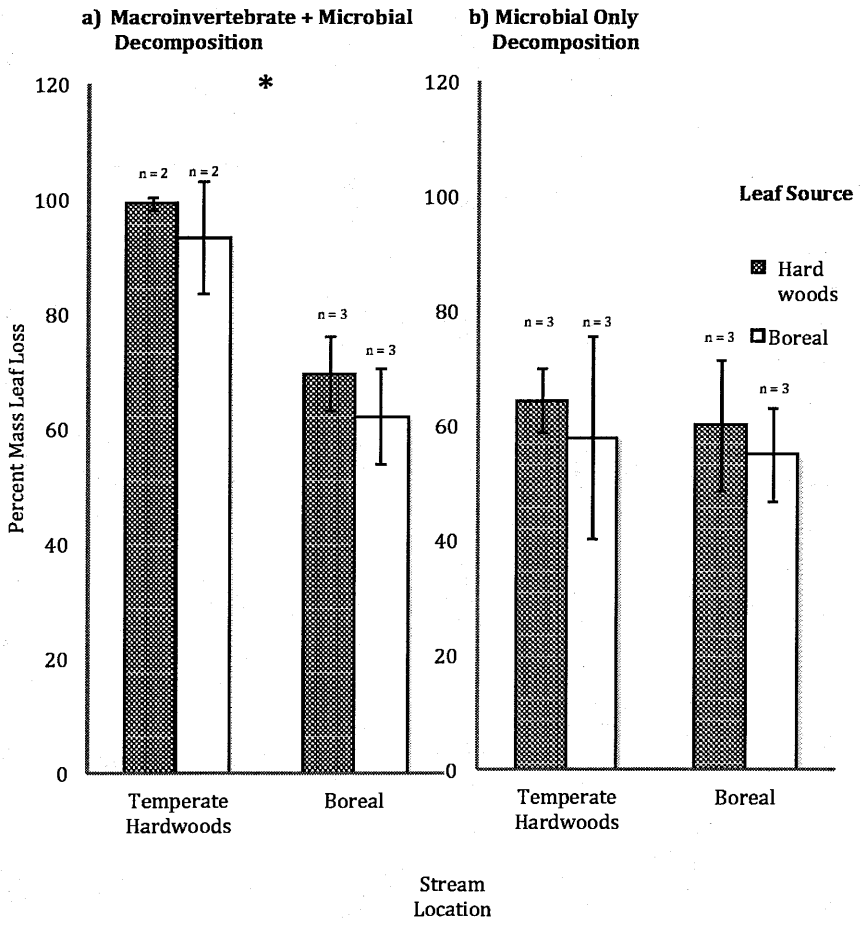

Fig. 1.4 Percent mass loss of alder leaves (*Alnus incana rugosa*) in a) coarse leaf litter bags (1 cm x 1cm) that allowed for both macroinvertebrate and microbial decomposition (PERMANOVA: Stream Location: Pseudo-F = 10.094, P = 0.016) and b) fine leaf litter bags (0.5 mm x 0.5 mm) that excluded macroinvertebrates and allowed for mostly microbial decomposition (PERMANOVA: Stream Location: Pseudo-F = 0.237, P = 0.645). * indicates significance between streams.

Table 1.4 Mean ± SD results for macroinvertebrate abundance, Shannon Diversity, Simpson's Evenness, and family richness (α-diversity). Abundance and diversity measures were reported for total macroinvertebrates and the orders Diptera, Ephemeroptera, Odonata, Plecoptera, and Trichoptera.

mean ± SD	Total Macroinvertebrates				Diptera			
	Abundance	Shannon Diversity	Simpson's Evenness	α-Diversity	Abundance	Shannon Diversity	Simpson's Evenness	α-Diversity
Stream Location								
Hardwoods	34.5 ± 19.4	1.7 ± 0.0	3.2 ± 0.0	3.5 ± 1.0	27.8 ± 16.2	0.08 ± 0.00	1.0 ± 0.0	1.0 ± 0.0
Boreal	22.3 ± 10.7	1.4 ± 0.2	2.9 ± 0.3	6.0 ± 1.5	11.7 ± 11.2	0.07 ± 0.01	1.0 ± 0.0	1.3 ± 0.5
Leaf Source								
Hardwoods	24.4. ± 14.9	1.5 ± 0.1	3.1 ± 0.1	5.2 ± 2.6	14.6 ± 14.0	0.07 ± 0.01	1.0 ± 0.0	1.4 ± 0.5
Boreal	30.0 ± 16.5	1.4 ± 0.2	2.9 ± 0.3	4.8 ± 0.8	21.6 ± 16.8	0.08 ± 0.01	1.0 ± 0.0	1.0 ± 0.0
SL x LS								
Hard. x Hard.	26.0 ± 21.2	1.6 ± 0.0	3.3 ± 0.0	3.0 ±1.4	19.5 ± 0.0	0.08 ± 0.00	1.0 ± 0.0	1.0 ± 0.0
Hard. x Boreal	43.0 ± 19.8	1.5 ± 0.0	3.2 ± 0.0	4.0 ± 0.0	36.0 ± 0.0	0.08 ± 0.00	1.0 ± 0.0	1.0 ± 0.0
Boreal x Hard.	23.3 ± 14.6	1.5 ± 0.0	3.1 ± 0.0	6.7 ± 2.1	11.3 ± 16.2	0.07 ± 0.00	1.0 ± 0.0	1.7 ± 0.6
Boreal x Boreal	21.3 ± 8.3	1.2 ± 0.2	2.7 ± 0.2	5.3 ± 0.6	12.0 ± 7.2	0.07 ± 0.01	1.1 ± 0.0	1.0 ± 0.0

mean ± SD	Ephemeroptera				Odonata			
	Abundance	Shannon Diversity	Simpson's Evenness	α-Diversity	Abundance	Shannon Diversity	Simpson's Evenness	α-Diversity
Stream Location								
Hardwoods	0.3 ± 0.5	1.7 ± 0.1	5.0 ± 0.4	0.3 ± 0.5	0.0 ± 0.0	0.5 ± 0.1	1.6 ± 0.1	0.0 ± 0.0
Boreal	6.3 ± 3.5	1.3 ± 0.2	3.6 ± 0.4	3.3 ± 1.0	0.7 ± 0.8	0.3 ± 0.0	1.4 ± 0.1	0.5 ± 0.5
Leaf Source								
Hardwoods	4.2 ± 4.3	1.6 ± 0.2	4.4 ± 0.8	2.2 ± 2.2	0.2 ± 0.4	0.4 ± 0.1	1.5 ± 0.1	0.2 ± 0.4
Boreal	3.6 ± 4.4	1.4 ± 0.2	3.9 ± 0.7	2.0 ± 1.6	0.6 ± 0.9	0.4 ± 0.1	1.4 ± 0.1	0.4 ± 0.5
SL x LS								
Hard. x Hard	0.0 ± 0.0	1.7 ± 0.0	5.3 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.0	1.6 ± 0.0	0.0 ± 0.0
Hard. x Boreal	0.5 ± 0.7	1.6 ± 0.0	4.6 ± 0.2	0.5 ± 0.7	0.0 ± 0.0	0.4 ± 0.1	1.5 ± 0.1	0.0 ± 0.0
Boreal x Hard.	7.0 ± 2.6	1.5 ± 0.1	3.9 ± 0.3	3.7 ± 1.2	0.3 ± 0.6	0.3 ± 0.0	1.4 ± 0.1	0.3 ± 0.6
Boreal x Boreal	5.7 ± 4.7	1.2 ± 0.0	3.4 ± 0.2	3.0 ± 1.0	1.0 ± 1.0	0.3 ± 0.1	1.4 ± 0.1	0.7 ± 0.6

mean ± SD	Plecoptera				Trichoptera
	Abundance	Shannon Diversity	Simpson's Evenness	α-Diversity	Abundance
Stream Location					
Hardwoods	6.3 ± 4.1	0.6 ± 0.0	1.5 ± 0.0	2.0 ± 0.8	12.3 ± 17.1
Boreal	3.7 ± 2.2	0.5 ± 0.1	1.5 ± 0.1	0.8 ± 0.4	18.7 ± 12.8
Leaf Source					
Hardwoods	5.2 ± 3.8	0.6 ± 0.0	1.6 ± 0.0	1.2 ± 0.4	15.6 ± 14.4
Boreal	4.2 ± 2.8	0.5 ± 0.2	1.5 ± 0.1	1.4 ± 1.1	16.6 ± 15.5
SL x LS					
Hard. x Hard.	6.0 ± 7.1	0.6 ± 0.0	1.5 ± 0.0	1.5 ± 0.7	19.5 ± 24.7
Hard x Boreal	6.5 ± 0.7	0.6 ± 0.0	1.6 ± 0.0	2.5 ± 0.7	5.0 ± 7.1
Boreal x Hard.	4.7 ± 1.5	0.6 ± 0.0	1.6 ± 0.0	1.0 ± 0.0	13.0 ± 9.0
Boreal x Boreal	2.7 ± 2.5	0.4 ± 0.1	1.5 ± 0.1	0.7 ± 0.6	24.3 ± 15.3

Table 1.5. Summary of simple regression results examining the correlation between percent leaf loss and Shannon Diversity in only local leaves, only regional leaves, and both leaf types for total macroinvertebrates and Ephemeroptera.

Shannon Diversity Regression Results	Total Macroinvertebrates			Ephemeroptera		
	Local	Regional	Both	Local	Regional	Both
R^2_{adj}	0.61	0.62	0.50	0.88	0.50	0.7466
P	0.074	0.071	**0.013**	**0.011**	0.111	**0.00126**

Table 1.6. Summary of simple regression results examining the correlation between percent leaf loss and α-Diversity in only local leaves, only regional leaves, and both leaf types for total macroinvertebrates and Ephemeroptera.

α-Diversity Regression Results	Total Macroinvertebrates			Ephemeroptera		
	Local	Regional	Both	Local	Regional	Both
R^2_{adj}	0.60	0.53	0.43	0.93	0.63	0.73
P	0.08	0.101	**0.023**	**0.005**	0.068	**0.001**

Table 1.7. Summary of simple regression results examining the correlation between percent leaf loss and Simpson's Evenness in only local leaves, only regional leaves, and both leaf types for total macroinvertebrates and Ephemeroptera.

Simpson's Evenness Regression Results	Total Macroinvertebrates			Ephemeroptera		
	Local	Regional	Both	Local	Regional	Both
R^2_{adj}	0.67	0.56	0.5435	0.80	0.47	0.74
P	0.06	0.091	**0.015**	**0.026**	0.121	**$9x10^{-4}$**

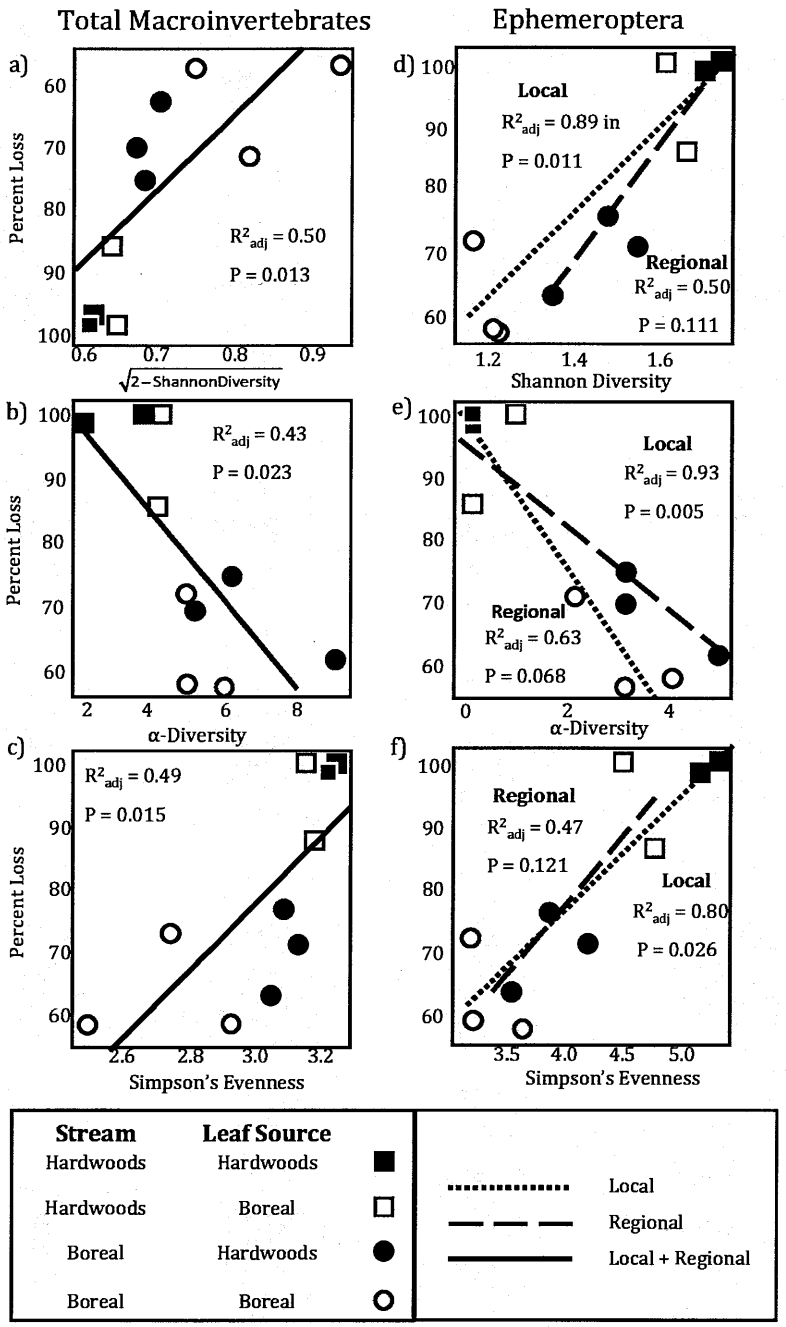
Total Macroinvertebrates
Ephemeroptera
a)
Percent Loss
R^2_{adj} = 0.50
P = 0.013
√2−ShannonDiversity
d)
Local
R^2_{adj} = 0.89 in
P = 0.011
Regional
R^2_{adj} = 0.50
P = 0.111
Shannon Diversity
b)
Percent Loss
R^2_{adj} = 0.43
P = 0.023
α-Diversity
e)
Local
R^2_{adj} = 0.93
P = 0.005
Regional
R^2_{adj} = 0.63
P = 0.068
α-Diversity
c)
Percent Loss
R^2_{adj} = 0.49
P = 0.015
Simpson's Evenness
f)
Regional
R^2_{adj} = 0.47
P = 0.121
Local
R^2_{adj} = 0.80
P = 0.026
Simpson's Evenness
Stream
Leaf Source
Hardwoods
Hardwoods
Hardwoods
Boreal
Boreal
Hardwoods
Boreal
Boreal
Local
Regional
Local + Regional

Fig. 1.5 Relationships between macroinvertebrate community diversity and decomposition for families across taxonomic orders (total macroinvertebrate community): **(a)** Shannon Diversity, **c)** α-diversity, **e)** Simpson's Evenness), and for families within the order Ephemeroptera: **(b)** Shannon Diversity; **d)** α-diversity; **f)** Simpson's Evenness. Significant regressions ($P<0.05$) are given for diversity-decomposition relationships on local source leaves and regional source leaves. In cases where neither leaf source was important on its own, regressions are given for both leaf sources combined.

When diversity-decomposition relationships were examined for families within each macroinvertebrate order and separately from the rest of the macroinvertebrate community, only the order Ephemeroptera was related to decomposition rate (Table 1.4, 1.8). For the Ephemeroptera, significant positive diversity-decomposition relationships were detected on local source leaves but not regional source leaves for Shannon Diversity (Fig. 1.5d) and Simpson's Evenness (Fig. 1.5f) indices (Tables 1.4-1.7). However, there was a negative relationship between α-diversity (taxon richness) and decomposition rate (Fig. 1.5e) on the local source leaves that mirrored the significant negative linear relationship that also occurred on the regional source leaves. We also looked at the relationship between biodiversity and decomposition for the Plecoptera order (Table A.5). We found that the Plecoptera followed a similar pattern the total macroinvertebrates (Table A.5). We did not test the Odonata group, as we only identified four individuals in the entire experiment belonging to this group, making it hard to distinguish any real pattern.

Although a number of explanatory variables were significantly related to decomposition in coarse mesh litter bags, this may reflect correlations between explanatory variable, such as differences in macroinvertebrate diversity between the two streams. We therefore competed our models against each other in a model selection framework, and concluded that decomposition was best explained by either stream identity or by Ephemoptera diversity (both models were selected to be in the plausible set: Table A.3).

Table 1.8. Results for macroinvertebrate abundance, Shannon Diversity, Simpson's Evenness, and family richness (α-diversity). Abundance and diversity measures were reported for total macroinvertebrates and the orders Diptera, Ephemeroptera, Odonata, Plecoptera, and Trichoptera. Results are from a PERMANOVA with stream location and leaf source as fixed effects under 999 permutations.

PERMANOVA	Total Macroinvertebrates				Diptera			
	Abundance	Shannon Diversity	Simpson's Evenness	α-Diversity	Abundance	Shannon Diversity	Simpson's Evenness	α-Diversity
d.f. effect	1	1	1	1	1	1	1	1
d.f. total	9	9	9	9	9	9	9	9
Stream Location								
Pseudo-F	0.295	7.346	11.570	8.631	3.003	3.446	1.388	2.4
P(perm)	0.609	**0.001**	**0.001**	**0.001**	0.144	0.113	0.545	0.258
Leaf Source								
Pseudo-F	0.204	3.990	6.250	0.778	1.146	0.106	1.388	2.4
P(perm)	0.634	**0.042**	**0.002**	0.535	0.338	0.873	0.46	.141
SL x LS								
Pseudo-F	0.401	2.358	2.994	1.764	0.271	0.106	1.388	2.4
P(perm)	0.56	0.155	0.091	0.175	0.671	0.87	0.46	0.135

PERMANOVA	Ephemeroptera				Odonata			
	Abundance	Shannon Diversity	Simpson's Evenness	α-Diversity	Abundance	Shannon Diversity	Simpson's Evenness	α-Diversity
d.f. effect	1	1	1	1	1	1	1	1
d.f. total	9	9	9	9	9	9	9	9
Stream Location								
Pseudo-F	33.094	72.017	51.678	36.294	2.648	21.236	24.005	2.7
P(perm)	**0.001**	**0.001**	**0.001**	**0.001**	0.18	**0.003**	**0.003**	0.168
Leaf Source								
Pseudo-F	0.349	19.734	8.901	0.850	0.480	0.836	1.045	0.3
P(perm)	0.739	**0.001**	**0.03**	0.515	0.514	0.385	0.367	0.635
SL x LS								
Pseudo-F	1.339	6.306	0.438	1.253	0.480	3.536	0.229	0.3
P(perm)	0.289	0.028	0.526	0.329	0.523	0.115	0.653	0.596

PERMANOVA	Plecoptera				Trichoptera
	Abundance	Shannon Diversity	Simpson's Evenness	α-Diversity	Abundance
d.f. effect	1	1	1	1	1
d.f. total	9	9	9	9	9
Stream Location					
Pseudo-F	0.452	3.717	0.345	6.953	1.539
P(perm)	0.564	0.011	0.537	**0.018**	0.244
Leaf Source					
Pseudo-F	4.13×10^{-2}	2.526	1.202	0.592	0.408
P(perm)	0.964	0.139	0.431	0.535	0.661
SL x LS					
Pseudo-F	1.377	2.064	1.666	2.178	1.142
P(perm)	0.263	0.21	0.298	0.166	0.332

Stream but not leaf source played a significant role in distinguishing the overall composition of macroinvertebrate families on the leaves in the leaf bags (multivariate PERMANOVA: Pseudo-F = 4.081, P = 0.022; NMDS: Fig. 1.6). Shannon Diversity of macroinvertebrate families across taxonomic orders on the leaf bags was determined by both stream and leaf source, but not an interaction between these effects (Table 1.8; Fig. 1.7a), as was also the case for Simpson's Evenness indices (Table 1.8; Fig. 1.7c). Shannon Diversity of the entire macroinvertebrate community was 1.2x greater in the temperate hardwood stream than in the boreal stream, and on temperate hardwood source leaves compared to boreal source leaves (Table 1.8; Fig. 1.7a). These patterns also held for Simpson's Evenness where the communities were more even in the temperate hardwood stream and on temperate hardwood leaves in both streams than in the boreal stream and on boreal leaves in both streams (Fig. 1.7c). Within litter bags, taxon richness (α-diversity) of the total macroinvertebrate community at the family level was determined only by stream and not leaf source (Table 1.8; Fig. 1.7b) where total local family richness was 1.7x greater in the boreal stream (Table 1.8; Fig. 1.7b).

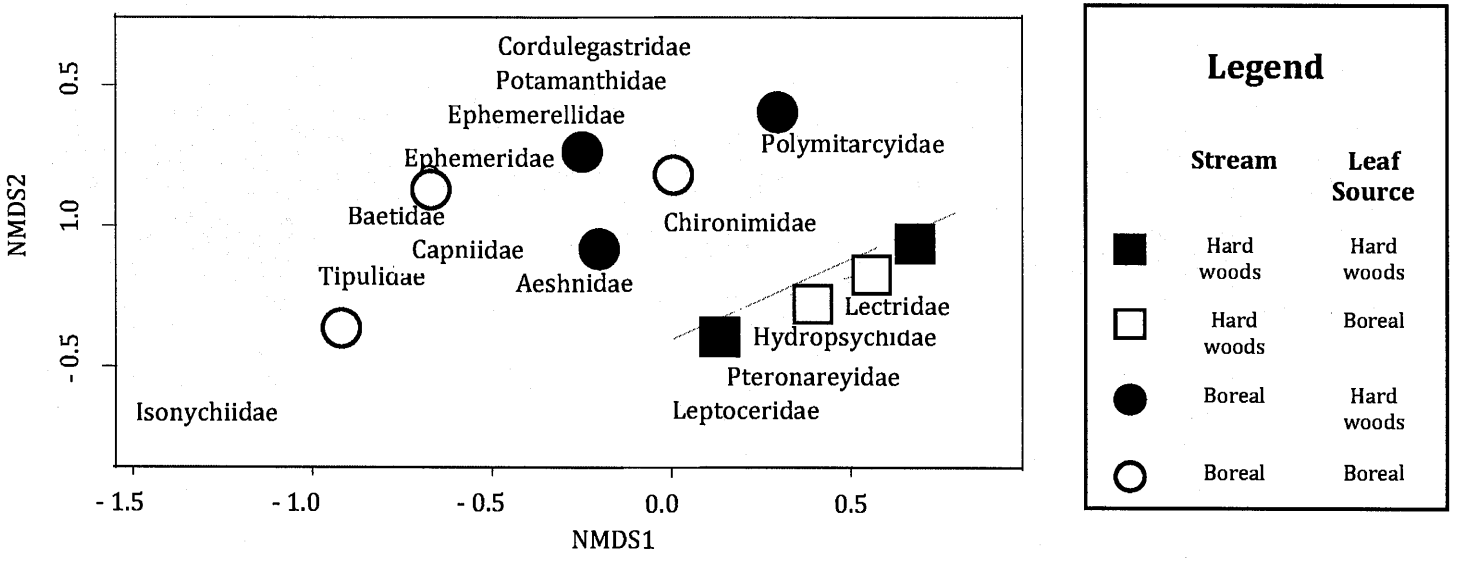

Fig. 1.6 Non-metric multidimensional scaling (NMDS) of families across macroinvertebrate orders for which total abundance was enumerated in the coarse-mesh leaf litter bags (1 cm x 1cm). Overall community composition was distinguished according to stream (squares = hardwoods; circles = boreal) but not leaf litter source (solid = hardwoods; open = boreal; P = 0.022).

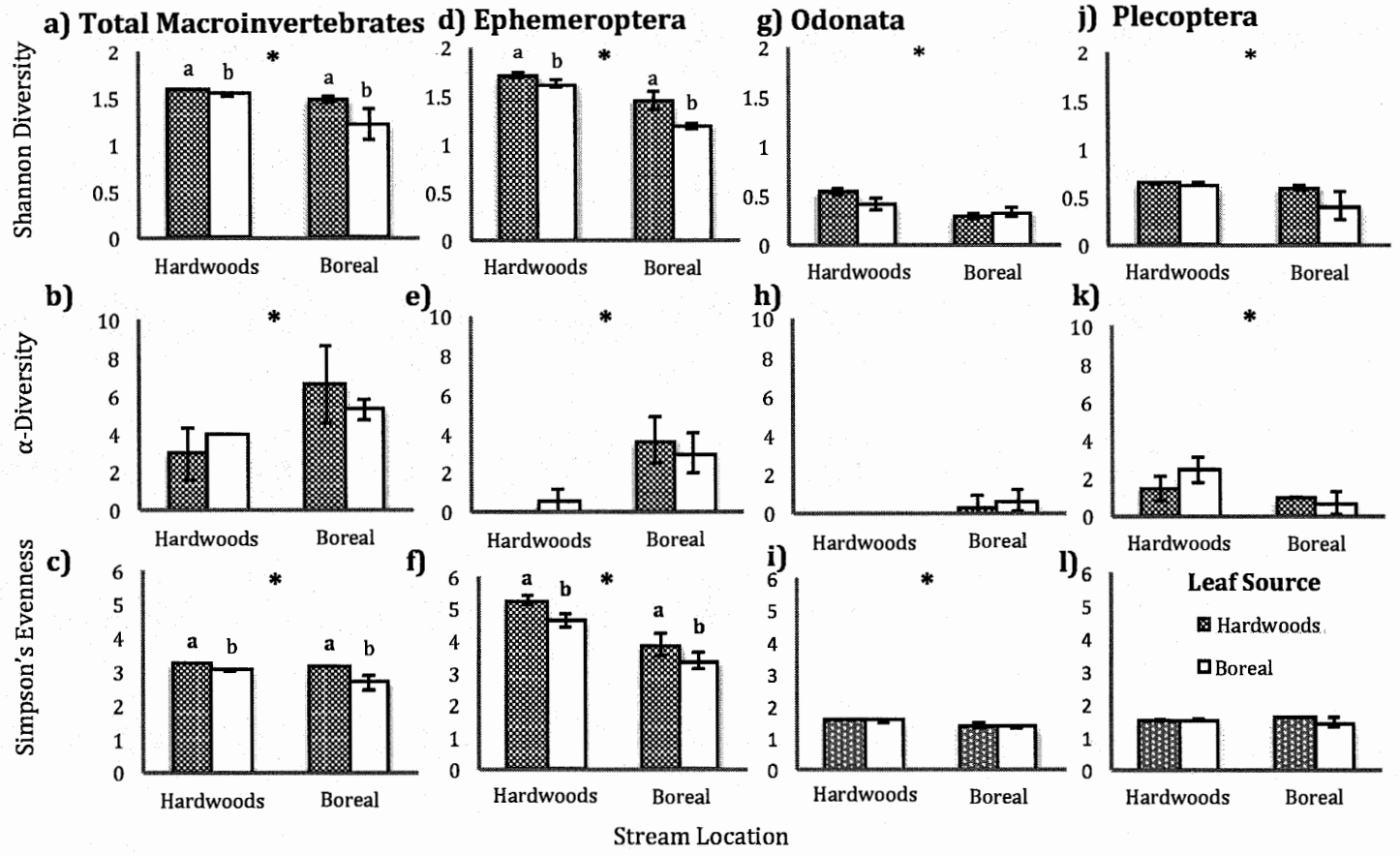

Fig. 1.7 PERMANOVA results of a) total macroinvertebrate Shannon Diversity b) total macroinvertebrate α-diversity, c) total macroinvertebrate Simpson's Evenness, d) Ephemeroptera Shannon Diversity, e) Ephemeroptera α-diversity, f) Ephemeroptera Simpson's Evenness, g) Odonata Shannon Diversity, h) Odonata α-diversity, i) Odonata Simpson's Evenness, j) Plecoptera Shannon Diversity, k) Plecoptera α-diversity, and l) Plecoptera Simson's Evenness, where * indicate significant differences between stream location and letters indicate differences between leaf litter sources ($P<0.05$) (Table 2.6). $N_{hardwoods\ stream} = 2$ per leaf litter source, $n_{boreal\ stream} = 3$ per leaf litter source.

Within each taxonomic order, the Shannon Diversity of families within the Orders Ephemeroptera, Odonata, and Plecoptera in the leaf bags depended on the stream (Table 1.8; Fig. 1.7d, g, j). In the Ephemeroptera, there was lower family diversity in the boreal stream compared to the temperate hardwood stream (Table 1.8; Fig. 1.7d). However, families within Odonata and Plecoptera were more diverse in the temperate hardwood forest stream compared to the boreal stream (Table 1.8; Fig. 1.7g, j). In terms of local family richness, main effects of stream were detected for Ephemeroptera and Plecoptera (Table 1.8). While Ephemeroptera family richness was greater in the boreal stream (Fig. 1.7e), family richness of Plecoptera was greater in the temperate hardwood stream (Fig. 1.7k). In terms of Simpson's Evenness, main effects of stream were detected for Ephemeroptera and Odonata (Table 1.8). Both the Ephemeroptera and Odonata echoed the total macroinvertebrate pattern, having higher evenness in the temperate hardwood stream (Fig. 1.7f, i). Main effects of leaf source were detected only for Ephemeroptera (Table 1.8) in which the temperate hardwood leaves had higher evenness compared to the boreal leaves (Fig. 1.7f).

The total abundance of macroinvertebrates did not differ between streams (Fig. 1.8). With the exception of the Order Ephemeroptera that was more abundant in the boreal forest stream compared to the temperate hardwood forest stream (Fig. 1.8), all other macroinvertebrate orders that were detected did not differ in abundance between study streams (Table 1.6).

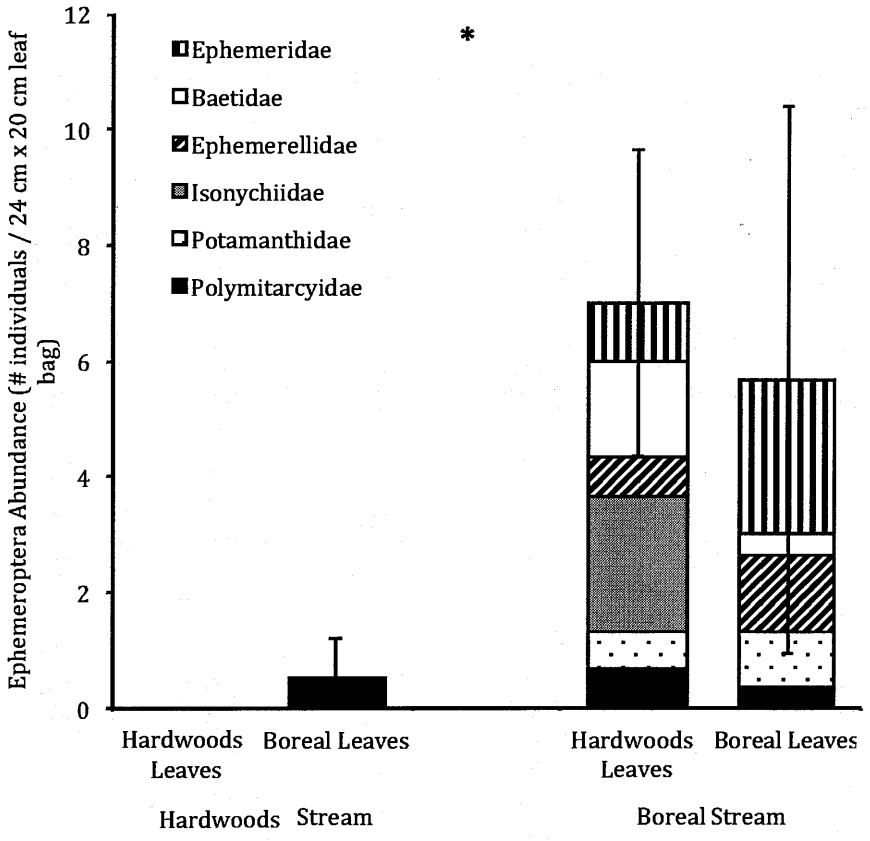

Fig. 1.8 Total abundance of families within the Ephemeroptera order (# individuals per 24 cm x 20 cm bag) in coarse leaf litter bags (1 cm x 1cm) between stream locations and leaf litter sources. * indicates significant difference between streams ($P<0.05$)

1.5 Discussion

Macroinvertebrate diversity in freshwater streams was correlated with the decomposition rate of leaf litter, but this relationship was driven by local stream conditions rather than the leaf litter source. There was no evidence to support 'home field advantage' effects associated with leaf litter source. Local stream conditions, such as differences in nutrients and the local quality of riparian vegetation, were likely key factors in determining differences in diversity, abundance, and composition of macroinvertebrate communities between the two study streams. Our study supports our alternative hypothesis (Fig. 1.1b) and other key research that has found little to no support for a 'home field advantage' in decomposer communities even at broad spatial scales (Veen et al. 2015a; Veen et al. 2015b). However, we also highlight how individual taxonomic groups may have specialized responses, such as 'home field advantage' effects in the Ephemeroptera. These 'home field advantage' effects would not be detected of the community is considered as an aggregate in biodiversity-ecosystem function relationships. This is important because while ecosystem functions, such as decomposition, can be preserved by functional redundancy among taxonomic groups (Wohl et al. 2004), specialized responses within certain taxonomic groups may have hidden or unmeasured consequences for community structure and ecosystem function (Duffy et al. 2007).

1.5.1 Biodiversity-decomposition relationships

Biodiversity-decomposition relationships in stream macroinvertebrates were driven by local stream conditions between two different biomes, and were not influenced by a 'home field advantage' associated with the source of leaf litter. This finding for the overall macroinvertebrate community did not support our null hypothesis where biodiversity influenced decomposition but the response between local versus regional source leaf litter was not different (Fig. 1.1b; Fig. 1.5a-c). The exception was Ephemeroptera in which there were positive relationships at the family-level with Shannon Diversity and Simpson's Evenness with respect to decomposition rate on local source leaf litter but not regional source leaf litter in the boreal stream (Fig. 1.1a; Fig. 1.5d, f). The difference in response to local versus regional source leaf litter within the Ephemeroptera in the boreal stream only may be related to i) differences in taxonomic composition of families or species or ii) specialised population-level responses. In our case, differences in the taxonomic composition of families played a role because of differences in the families that colonized the bags from different leaf sources in the boreal stream (Fig. 1.8). However, we caution that the effects of stream identity cannot be distinguished from the effects of Ephemeroptera, as both models were found to be equally plausible using model selection. Future research could investigate community and population-level specialisation within Ephemeroptera within and between streams.

Our findings support the hypothesis that biodiversity can influence a key ecosystem function, stream decomposition, and this result is supported by many other studies (Tilman et al. 1996; Tilman et al. 1997; van der Heijden et al. 1998;

Dang et al. 2005; Balvanera et al. 2006; Cardinale et al. 2006; Cadotte et al. 2008, Lecerf and Chauvet 2008; Isbell et al. 2011; Boyero et al. 2012; Veen et al. 2015a). We found that there were positive relationships between Simpson's Evenness and decomposition rate (Fig. 1.5c, f). This finding is consistent with other studies that have pointed to the importance of taxon evenness in biodiversity relationships with decomposition (Dangles and Malmqvist 2004; Kominoski et al. 2009). However, we also found that taxon richness was negatively related with decomposition rate (Fig. 1.5b, e), contrary to other research which has found that the number of different species and their functional roles are the main drivers of a positive relationship between biodiversity and decomposition (Dimitrakopoulos 2010; Baiser and Lockwood 2011; Flynn et al. 2011). We cannot discount here the possibility that invertebrates left our litterbags when very little leaf litter remained, causing such a negative relationship. Note that although some litterbags lost 100% of litter, this loss includes the removal of leaves at the end for DNA analyses for another experiment, indicating that there was some leaf litter remaining in all bags. We found that the direction of the response of decomposition rate to biodiversity metrics depended on the taxonomic group considered. There was an overall positive relationship in the total macroinvertebrate community between biodiversity and decomposition (Fig. 1.5a), which also occurred in the order Ephemeroptera (Fig. 1.5d). For other macroinvertebrate orders such as the order Plecoptera there was a positive relationship between Shannon Diversity and decomposition similar to the total macroinvertebrate regression (Table A.5), but it was weaker than the relationship of Shannon Diversity in total macroivertebrate families and families within the Ephemeroptera. The contradictory positive and negative responses of decomposition to species richness and evenness in different studies and across taxa illustrate the complexity of understanding how biodiversity impacts decomposition.

1.5.2 No evidence for 'home field advantage'

The lack of 'home field advantage' on local versus regional source leaves between regionally-distant macroinvertebrate decomposer communities was unexpected in our study because i) we employed a single species of speckled alder (*Alnus incana rugosa*), ii) there is a large geographical distance and environmental differences associated with the different biomes where our study streams and leaf litter sources were located (temperate hardwood versus boreal forest; Fig. 1.2), and iii) there were differences in secondary compounds (hemicellulose and lignin) between regional sources of speckled alder that could have potentially produced a 'home field advantage' (Fig. 1.3). 'Home field advantage' has most often been detected in studies that implement single-species leaf sources compared to mixed vegetation community sources because species mixtures can cause opposing effects that cancel each other out at the community level (Veen et al. 2015b). 'Home field advantage' has also most often been reported by studies in which there are large distances or environmental differences between sites (Veen et al. 2015b). Together, these observations suggest that home field advantage effects are not relevant at the community level over landscape scales; rather, they may only be relevant for single litter species contrasted at regional scales.

Our study streams are located in two different biomes and are geographically distant by 540 km (Fig. 1.2). We found differences in the physical-chemical conditions of streams (nutrients, DOC, and bacterial production; Table 1.1) as well as in the lignin and hemicellulose concentration between the two leaf litter sources (Fig. 1.3). Other studies have also found great variation in leaf chemical

concentration and stream conditions over large areas, (Mulholland et al. 2001; Way and Oren 2010). Despite these differences in both streams and litter chemistry, we did not find evidence for a 'home field advantage'. In fact, there was no difference in the decomposition of the two litter origins, despite higher lignin concentration in the hardwood litter. Lignin is less digestible than cellulose (Van Soest and McQueen 1973) and is generally associated with reduced decomposition (Horner et al. 1988; Shindler and Gessner 2000). Our results contrasts with studies that have shown 'home field advantage' in stream macroinvertebrate communities associated with large differences in litter chemistry and stream conditions (LeRoy and Marks 2006; Jackrel and Wootton 2014). However, another study on decomposition in the Artic found that neither stream conditions nor leaf characteristics correlated well with the presence and strength of 'home field advantage' (Veen et al. 2015a). Our findings are consistent with this latter study: differences in stream conditions and leaf chemistry do not necessarily produce 'home field advantage' effects in local macroinvertebrate decomposer communities, even between regionally-distant streams and leaf litter sources.

Differences in chemical traits of leaf sources in our study also had the potential to predispose local macroinvertebrate communities to favor local source leaves in each of the respective streams. In terms of secondary compounds in the alder leaves, hemicellulose concentrations were higher in the boreal source leaves and lignin concentrations were higher in the temperate hardwood source leaves during our experiment. Both hemicellulose and lignin are known to slow decomposition rates (Aerts 1997; Wardle et al. 1998; LeRoy and Marks 2006; Johnson et al. 2007; Rahman et al. 2013), although some studies have suggested otherwise (Vivanco and Austin 2008). Macroinvertebrates play an essential role

in breaking down cellulose and hemicellulose in leaves as well as in mobilizing nutrients in streams (Schaller 2013), and so were expected to respond to differences between leaf sources in these compounds. However, there was no support for an overall 'home field advantage' in the total macroinvertebrate community despite differences in these secondary compounds between the two regional leaf sources.

We caution that litter quality is not only affected by secondary compounds, but also nutrient concentrations in leaves (Aerts 1997; Ostrofsky 1997; LeRoy and Marks 2006; Rahman et al. 2013), which were not measured in this study. Other studies have found that nutrient concentration in leaves can be more important than stream nutrient conditions with regards to the biodiversity of the macroinvertebrate decomposer community associated with the leaves (LeRoy and Marks 2006; Ward et al. 2015). Although we are presently missing this piece of information, it may contribute to explaining the differences between leaf sources in total macroivertebrate biodiversity measures that we observed within each of the streams.

1.5.3 Local stream effects

The temperate hardwood stream had higher temperature, higher nutrient levels and bacterial production than the boreal stream (Table 1.1). Decomposition is known to increase with temperature (Moore 1986; McHale et al. 1998; Bothwell 2014). Higher concentrations of nutrients in streams are associated with higher

rates of stream metabolism (Mulholland et al. 2001) and decomposition (Gulis et al. 2006, Hagen et al. 2006). Higher nutrient concentrations and bacterial production in the temperate hardwood stream may have strongly contributed to more rapid decomposition rates in the temperate hardwood stream compared to the boreal stream (Fig. 1.4). The hardwood stream also had a greater proportion of decomposition due to macroinvertebrates, as assessed by the difference in decomposition between coarse and fine litter bags. Although mesh size may also affect decomposition by altering abiotic conditions inside the litter bag, methodological studies have concluded such artifacts are minor (Bokhurst and Wardle 2013).

Macroinvertebrate abundance did not explain the difference in decomposition between streams because the total number of macroinvertebrates that colonized the litter bags was higher in the boreal stream whereas decomposition was lower. However, we found that Shannon Diversity was higher in the temperate hardwood stream across orders of macroinvertebrates. This was also the case for Simpson's Evenness, but not for local family richness (α-diversity) that was lower in the temperate hardwood stream compared to the boreal stream across all orders of macroinvertebrates (Fig. 1.7). It is possible that the greater nutrient enrichment of the temperate hardwood stream played a role in enhancing the diversity and evenness of the macroinvertebrate community in our study. Other studies have found that nutrients in streams can be associated with higher taxon richness (Matthaei et al. 2010) and/or evenness (LeRoy and Marks 2006), although this effect could be dampened by reduced flow rate and perhaps other variables not taken into account in each of the streams (Matthaei et al. 2010).

Differences in functional roles of different taxonomic groups of macroinvertebrates can have a strong impact on decomposition (Gessner et al. 2010; Handa et al. 2014). Odonata are mostly comprised of predators that typically prey on other macroinvertebrates (Poff et al. 2006; Gessner et al. 2010; Ferreira et al. 2014). Plecoptera are typically shredders in the decomposition cycle, responsible for breaking the leaves apart and ingesting larger pieces of detritus (Heino and Mykrä 2008; Ferreira et al. 2014). Ephemeroptera are primarily collectors, who are more likely to feed on fine particulate matter (Brittain and Salveit 1989; Poff et al. 2006). A separate analysis of functional groups within these macroinvertebrate communities from this study detected that filterers-collectors were more abundant in the temperate hardwood stream than in the boreal stream regardless of leaf litter source (Dodier 2016). The greater abundance of this overall functional group in the temperate hardwood stream may be a function of greater palatability of leaves in the temperate hardwood stream compared to the boreal stream, potentially leading to faster decomposition rates. Future research could incorporate measures of functional diversity to understand how macroinvertebrate biodiversity-decomposition relationships may differ between streams and between local and regional sources of litter; to the best of our knowledge this has rarely been attempted (but see Dodier 2016).

By working with an animal system and in a more natural context, our study provides a unique perspective to a body of literature that is dominated by plant studies and experiments in more simplified systems (Schwartz et al. 2000; Duffy 2002; Smith and Knapp 2003; Srivastava and Vellend 2005; Roussel et al. 2008; Grman et al. 2010; Tilman et al. 2012).

1.6 Conclusion

The link between biodiversity and ecosystem function, and understanding how this relationship varies within and between ecosystems, is a critical component of preserving ecosystem services on which humans rely (Daily and Matson 2008). Our findings indicate that there is limited evidence to support a relationship between family diversity and decomposition in the macroinvertebrate decomposer community. However, our study shows little support for any association between macroinvertebrate composition and leaf litter origin, although Ephemeroptera diversity was associated with higher decomposition of home litter. My study adds further evidence that 'home field advantage' seems to be minor in decomposition and does not seem to be universal. This study is unique in considering this question in northern temperate streams; most previous work has been in Europe or mid-Western USA. Future research could test if the biodiversity-decomposition patterns in macroinvertebrates that we detected between a hardwood stream and a boreal stream are consistent in other streams between these biomes, or if our findings are more representative of site-specific differences within biomes. The global loss of biodiversity may disrupt a number of ecosystem functions, either by exacerbating the predicted changes of these functions from climate change, or changing the outcome of the climate change (Daily and Matson 2008; Ehrlich and Ehrlich 2013; Ceballos et al. 2015). Many macroinvertebrate groups in streams are comprised of insect larvae (Gessner et al. 2010), and insect diversity is presently in global decline (Chapin III et al. 2000; Thomas et al. 2004). If biodiversity is positively linked to function (i.e. decomposition; Handa et al. 2014), then stream decomposition rates may be reduced as global insect diversity continues to be lost in an age of climate change and anthropogenic

impact. Alternatively, decomposition may be robust to changes in insect diversity because of functional redundancy or strong effects of microbial decomposition (Ruesink and Srivastava 2001). A major challenge for ecology is determining the context in which biodiversity loss triggers declines in function.

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CONCLUSION

My thesis has broadened our understanding of how biodiversity and decomposition link and other factors that may influence this relationship. Chapter 2 allowed us to better understand both the biodiversity and ecosystem function relationship and 'home field advantage' across two biomes. This, in turn, enabled us to expand our knowledge of these hypotheses on larger scales. Our study has shown that even when looking for a 'home field advantage' in scenarios that are more likely to have a 'home field advantage', there is difficulty finding one (Fig. 1.5; Veen et al. 2015b). The scale of our study ranging across two biomes has allowed us to further support the importance of some biodiversity measures, such as Shannon Diversity and Simpson's Evenness, in increasing decomposition (Fig. 1.5). As we saw that taxon richness was negatively correlated with decomposition, our study supports more research focusing on the importance of functional diversity in ecosystem function research, especially biodiversity (Fig. 1.5). We also saw that some orders' biodiversity was more likely to be correlated to decomposition than others (i.e. Ephemeroptera), indicating that a future focus on specific taxa should be encouraged. As Ephemeroptera are often used to infer habitat quality, it is reassuring to see that their biodiversity is related to an ecosystem function, like decomposition (Landa and Soldan 1991; Lydy et al. 2000).

My study was conducted during the summer despite the fact that most similar studies are conducted in the fall when leaf litter decomposition typically occurs. The fresh, non-senesced leaves that were used for my summer experiment have

a different chemical composition compared to leaves that senesce in the fall (Fig. 1.3). Seasonally, there was no difference between summer and fall leaf toughness for either location (Boreal leaves: $t_9 = 1.55$, $P = 0.156$; Temperate hardwood leaves: $t_9 = 2.05$, $P = 0.071$). However, hemicellulose concentrations varied seasonally between leaf sources: the fall levels of hemicellulose were significantly different in both leaf types between summer and fall leaves, with hemicellulose being higher in summer leaves compared to fall leaves (Boreal leaves: $t_4 = 16.88$, $P = 0.0001$; Temperate hardwood leaves: $t_4 = 3.06$, $P = 0.038$; Fig. A.4). Cellulose levels were lower in fall leaves compared to summer leaves for both leaf sources (Boreal leaves: $t_4 = 7.67$, $P = 0.002$; Temperate hardwood leaves: $t_4 = 2.91$, $P = 0.044$; Fig. A.4). In contrast, lignin was lower in summer leaves compared to fall leaves for both leaf sources (Boreal leaves: $t_4 = 10.28$, $P = 0.001$; Temperate hardwood leaves: $t_4 = 4.28$, $P = 0.013$; Fig. A.4). Differences in leaf chemistry of fresh summer leaves versus fall senescing leaves have been thoroughly described in the scientific literature (Aerts 1999; Eckstein et al. 1999). Therefore, it is possible that macroinvertebrate communities may have responded to the leaf source treatment differently in summer versus fall. However, it is also possible that seasonal differences such as temperature and timing of leaf senescence between the two biomes may play a stronger role than any leaf source effect in fall. Consequently, the lack of 'home field advantage' associated with leaf source in summer is likely a conservative measure, and could potentially be weaker in fall because of the strength of seasonality.

Our study has expanded our understanding of the role of macroinvertebrate abundance and diversity in decomposition, indicating some evidence for an association of overall diversity (Shannon Diversity and Simpson's Evenness) and decomposition. The role of the microbial community – bacteria and fungi – is

also important to understand and deserves more attention in the future. The microbial decomposer community accounts for approximately 20% of all decomposition and is important in priming the organic material for macroinvertebrate decomposers (Gulis and Suberkropp 2003; Gessner et al. 2010). Although we did not find any difference in microbial decomposition rates between streams and leaf sources (Fig. 1.6), this does not mean that there were no differences in either abundance or biodiversity of fungi and bacteria between sites. A study by Hättenschwiler et al. (2005) identified that the relationship between microbial biodiversity and decomposition was poorly understood. A review by McGuire and Treseder (2010) came to a similar conclusion. For example, a study by Dang et al. (2005) did not find a relationship between fungal diversity and decomposition, but they performed a microcosm experiment where they were reliant on fungal species that reproduce using spores, which is not representative of all fungal groups (Nikolcheva and Bärlocher 2004; Seena et al. 2010; Marano et al. 2011; Duarte et al. 2013). While bacteria comprise a small fraction of microbial decomposition (Gulis and Suberkropp 2003; Gessner et al. 2010), very little is known about their biodiversity in decomposition because it is difficult to identify bacteria due to limitations in the ability to culture certain groups, a similar issue that is encountered when identifying fungi (Das et al. 2007). With recent advances in DNA barcoding (Nikolcheva and Bärlocher 2004; Das et al. 2007; Duarte et al. 2009) it is anticipated that there will be more studies focused on the role of microbial biodiversity in decomposition. These advances make it possible to create a more complete picture of the microbial community without worrying on the ability of species to be cultured or to produce spores (Nikolcheva and Bärlocher 2004; Duarte et al. 2009). It is essential to have a clear view of how biodiversity in all decomposer groups affects decomposition to properly predict how perturbations to any of those decomposers will affect this process.

In this study, I explored how a novel concept such as 'home field advantage' may change our understanding of the biodiversity and ecosystem function relationship as well as the process of decomposition. For instance, if 'home field advantage' influences the decomposition process, it must be taken into account in ecosystem restoration projects. Restoring ecosystems is becoming an increasingly frequently used tool in conservation (Suding et al. 2015). Most often, restoration projects need to import species from donor populations that would be have been found in the area prior to disturbance to rehabilitate the area (Seddon and Soorae 1999; Wilcock and Jennings 1999; van Katwijk et al. 2009; Schröder and Prasse 2013). Importing plant species from populations far from the area where restoration is occurring would have an impact on the decomposition cycle in a case where 'home field advantage' is occurring, as has been documented in marine systems (van Katwijk et al. 2009; Schröder and Prasse 2013).

In the case of climate change, understanding both 'home field advantage' and the link between biodiversity and decomposition is imperative in predicting how climate change will impact different ecosystem functions (Irons III et al. 1994; Fierer et al. 2005; Davidson and Janssens 2006). Climate change may increase decomposition rate in some instances, such as increase moisture levels (Butenschoen et al. 2011; Salinas et al. 2011). However, if 'home field advantage' is a widespread phenomenon, then this may potentially reduce the increase in the rate of nutrient cycling. Climate change is predicted to shift the distribution of species towards the poles (Chen et al. 2011), which may change the local population make-up, thus potentially reducing local optimization for the decomposer community if taxa do not track changes in leaf litter composition along with other physico-chemical changes within streams. At the same time as

climate change, there is presently a huge reduction in biodiversity that is heavily impacting many groups of species, including insects (Chapin III et al. 2000; Thomas et al. 2004), adding further complexity in predicting the future of ecosystem functions. If biodiversity is positively linked to function (i.e. decomposition) (Tilman et al. 1996; Schwartz et al. 2000; Balvanera et al. 2006; Srivastava et al. 2009), then decomposition rates may be reduced and potentially counteract the predicted effect of increased temperature on decomposition rate (Butenschoen et al. 2011; Salinas et al. 2011). If both 'home field advantage' and biodiversity are influencing the decomposition, than these factors together may change how decomposition will be affected by global climate change. However, in my study, there was little evidence of a 'home field advantage' associated with the source of speckled alder leaf litter. These results are supported by many other studies in the decomposition literature, and so contribute to overall support for a lack of 'home field advantage' in aquatic decomposition. Moreover, leaf litter is comprised of many plant species in nature, and so even if 'home field advantage' is associated with certain plant taxa at the intraspecific level, other plant species with no 'home field advantage' effect may cancel out an overall signature of 'home field advantage' at the community level in the plant leaf litter (Veen et al. 2015b).

I found no evidence for a 'home field advantage' in aquatic decomposition of riparian alder leaves in freshwater streams even under conditions where we would most expect to find evidence of a home field advantage: single litter species, regionally distant streams, differences in litter chemistry between sites. Thus this study adds to a growing body of literature doubting 'home field advantage' in decomposition systems (Gießelmann et al. 2011; St John et al. 2011; Freschet et al. 2012; Makkonen et al. 2012). Moreover, this study extends

the literature by considering aquatic and boreal systems, neither of which are well represented in the home field advantage literature (Wang et al. 2013; Veen et al. 2015b). Although my thesis did not support the 'home field advantage' hypothesis, it did add more evidence for the biodiversity-ecosystem function hypothesis (Tilman et al. 1996; Tilman et al. 1997; van der Heijden et al. 1998; Balvanera et al. 2006; Cardinale et al. 2006; Cadotte et al. 2008; Cardinale et al. 2011; Isbell et al. 2011). Further research is necessary to understand how biodiversity is impacting decomposition to help protect this essential process in the future. Such research should address questions related to seasonality and variation within and between biomes at regional scales. Moreover, there is a need to understand biodiversity-ecosystem function relationships within understudied components of the decomposer community, such as bacteria and fungi.

APPENDIX A

Table A.1. Summary of individual macroinvertebrates counted in fine mesh (0.25mm^2) leaf litter bags during reciprocal transplant.

		Stream Site	Boreal	Boreal	Boreal	Boreal	Boreal	Boreal
		Leaf				Hardwood	Hardwood	Hardwood
Order	Family	Source	Boreal	Boreal	Boreal	s	s	s
Plecoptera	Capniidae		0	0	13	4	2	8
	Pteronareyidae		0	0	0	0	0	0
Ephemeroptera	Polymitarcyidae		0	0	0	0	0	1
	Potamanthidae		2	0	0	0	0	0
	Ephemerellidae		1	0	1	0	3	1
	Baetidae		1	0	0	0	0	2
Trichoptera	Unknown		23	0	18	47	13	46
	Rhacophilidae		0	0	1	0	0	0
Diptera	Chironimidae		11	9	4	4	11	12
	Tipulidae		1	0	0	0	0	0
Totals			39	9	37	55	29	70

Order	Family	Stream Site	Hardwoods	Hardwoods	Hardwoods	Hardwoods	Hardwoods	Hardwoods
		Leaf Source	Boreal	Boreal	Boreal	Hardwoods	Hardwoods	Hardwoods
Plecoptera	Capniidae		1	0	0	0	0	0
	Pteronareyidae		0	1	0	0	0	0
Ephemeroptera	Polymitarcyidae		0	0	0	1	0	0
	Potamanthidae		0	0	0	0	0	0
	Ephemerellidae		0	0	0	1	0	0
	Baetidae		0	0	0	0	0	0
Trichoptera	Unknown		1	4	0	0	3	1
	Rhacophilidae		0	0	0	0	0	0
Diptera	Chironimidae		19	26	5	15	13	10
	Tipulidae		0	0	1	2	0	0
Totals			21	31	6	19	16	11

Table A.2. Summary of macroinvertebrate community in coarse mesh (1cm^2) bags in a reciprocal leaf litter transplant. Numbers indicate the individuals counted in each family in each bag.

Order	Family	Stream Location Leaf Source	Boreal Boreal	Boreal Boreal	Boreal Boreal	Boreal Hardwoods	Boreal Hardwoods
Plecoptera	Lectridae		0	0	0	0	0
	Capniidae		5	3	0	3	5
	Pteronareyidae		0	0	0	0	0
Ephemeroptera	Polymitarcyidae		0	0	1	2	0
	Potamanthidae		2	0	1	1	0
	Isonychiidae		0	0	0	0	7
	Ephemerellidae		2	1	1	1	0
	Baetidae		0	1	0	1	1
	Ephemeridae		7	0	1	1	2
Odonata	Cordulegastridae		2	0	0	1	0
	Aeshnidae		0	1	0	0	0
Trichoptera	Unknown		7	30	36	22	4
	Leptoceridae		0	0	0	0	0
Diptera	Chironimidae		10	6	20	28	1
	Tipulidae		0	0	0	2	1
Coleoptera	Eulichadidae		0	0	0	0	0
Total			35	42	60	62	21

Order	Family	Stream Location Leaf Source	Boreal Hardwoods	Hardwoods Boreal	Hardwoods Boreal	Hardwoods Hardwoods	Hardwoods Hardwoods
Plecoptera	Lectridae		0	4	1	1	0
	Capniidae		6	3	3	0	9
	Pteronareyidae		0	0	2	0	2
Ephemeroptera	Polymitarcyidae		0	1	1	0	0
	Potamanthidae		1	0	0	0	0
	Isonychiidae		0	0	0	0	0
	Ephemerellidae		1	0	0	0	0
	Baetidae		3	0	0	0	0
	Ephemeridae		0	0	0	0	0
Odonata	Cordulegastridae		0	0	0	0	0
	Aeshnidae		0	0	0	0	0
Trichoptera	Unknown		13	0	0	37	1
	Leptoceridae		0	10	0	0	1
Diptera	Chironimidae		2	49	23	10	29
	Tipulidae		0	0	0	0	0
Coleoptera	Eulichadidae		0	0	0	0	1
Total			13	57	29	48	43

Table A.3. Summary of AIC_c model selection results where models explain leaf litter decomposition in a reciprocal transplant. Bold indicates selected models.

Model	logLik	AIC_c	Delta	Weight
Stream Site	-33.720	77.4	**0.00**	0.429
Ephemeroptera Shannon Diversity	-34.604	79.2	**1.77**	0.177
Ephemeroptera Taxon Richness	-34.607	79.2	**1.77**	0.177
Ephemeroptera Simpson's Evenness	-35.156	80.3	2.87	0.102
Stream Site + Leaf Source	-32.469	80.9	3.50	0.075
Total Shannon Diversity	-36.878	83.8	6.32	0.018
Total Simpson's Evenness	-37.095	84.2	6.75	0.015
Total Taxon Richness	-38.245	86.5	9.05	0.005
Stream Site x Leaf Source	-32.127	89.3	11.81	0.001
Null Model	-41.927	89.6	12.13	0.001
Leaf Source	-41.697	93.4	15.95	0.000

Table A.4. Mean ± SD percentage composition of leaf chemistry from summer experiment and fall samples. Paired T-test (df = 4) between seasons within biomes. Significant differences are bolded.

Leaf Source	% Hemicellulose	% Cellulose	% Lignin
Hardwoods			
Summer 2014	40.1 ± 0.4	33.7 ± 0.6	23.0 ± 0.2
Fall 2015	31.2 ± 3.2	28.8 ± 2.8	36.0 ± 5.2
T-value	5.2	2.9	4.3
P	**0.007**	**0.038**	**0.013**
Boreal			
Summer 2014	52.6 ± 0.9	33.8 ± 0.5	8.0 ± 1.1
Fall 2015	43.8 ± 1.7	26.7± 1.5	27.7 ± 3.1
T-value	8.1	7.7	10.3
P	**0.001**	**0.002**	**0.0005**

Table A.5. Summary of simple regression results examining the correlation between percent leaf loss and Shannon Diversity, α-Diversity, Simpson's Evenness in only local leaves, only regional leaves, and both leaf types for Plecoptera.

	Shannon Diversity			α-Diversity			Simpson's Evenness		
	Local	Regional	Both	Local	Regional	Both	Local	Regional	Both
R^2_{adj}	0.66	0.33	0.50	0.33	0.29	0.33	-0.02	0.24	-0.012
P	0.0595	0.181	**0.014**	0.182	0.202	**0.047**	0.412	0.231	0.372

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